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Regeneration ecology of oak in eastern Iowa

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PROBLEM SUMMARY

Regenerating the oak forests in eastern Iowa has been a major problem for decades. The oak forests in eastern Iowa occur at the transition of three major ecoregions and tend to be continually disturbed (Bailey, 1981). Oak in this area has been cited as an ecologically "unstable" species group and has been found to be difficult to manage effectively (Sander, 1977). Foresters and landowners have had difficulties in establishing young oaks under oak canopies. Market preference and traditional forest values continue to favor the objective of regenerating the oak forest in eastern Iowa.

The silvicultural treatments for regenerating white (Quercus alba L.)and red (Quercus rubra L.) oak in eastern Iowa have traditionally followed the prescriptions of Roach and Gingrich (1968), Sander (1977), and Barrett (1980). The stands have been regenerated using either clear-cutting or various types of shelterwood. In practical application, these methods of regeneration have led to undesirable species conversion of stands, extended rotations, and inconsistent production of desirable seedlings. Sugar maple (Acer saccharum Marsh., A. nigrum Michx., and their crosses), a less desirable species group in this area, has moved into the understory of oak stands and seems to

minimize oak regeneration. The conclusion drawn from the field has been that oak forest regeneration by "standard" techniques does not consistently work.

Because of the special biotic-environmental limitations on oak sites in eastern Iowa, coupled with volatile oak reproduction cycles, reproducing oak forests is a major problem. To regenerate oak, special care must be taken with the particular site and species interactions present. This study determines some of the active relationships between oak regeneration, the forest community, and the specific site. An interpretation of the regeneration ecology of white oak and red oak was made within the oak forests of eastern Iowa by determining the relationships between regeneration and the characteristics of the stand and site, and by evaluating the potential for active management.

LITERATURE REVIEW

Introduction

The following literature review section is divided into two parts. The first part is a general review of the most current concepts governing forest succession and provides the basis for the successional discussion later in this dissertation. The second part covers current silvicultural systems for regenerating oak and closely associated problems.

Forest Succession

Changing species composition of deciduous forests through time affects forest use. Management of forested sites has focused on continuous maximization of potential benefits over time. To accomplish "proper" management, the past, present, and potential composition may be assumed to be more or less mirrored in the present forest. The future forest will depend solely on the survival of tree propagules and their growth. Patterns of differential species survival and growth will probably affect the future trees, as they probably affected the present trees. Understanding species

patterning over time will provide insights into how forests can be manipulated to provide maximum benefits over time and preferential survival and growth of crop species relative to weed species.

Succession arises due to the differential reproduction, survival, and growth of a set of species. Regeneration is the vehicle for moving succession. Without successful regeneration, forest succession cannot occur. Because of this tie between succession and regeneration, understanding one can lead to a better understanding of the other. In forest stand management, regeneration is critical for the continuous yield from forested sites, and must be put into a successional context to prevent management errors. Forest management practice should magnify the natural fluctuations of species composition. The rules of the regeneration "game" are outlined by the interaction between species and sites and are called succession.

The purpose of critically examining successional patterns is to understand the natural shifts in composition that would occur after disturbance in a forest. Once disturbance effects are understood, anthropological disturbances, such as harvesting, thinning, or prescribed fire, can be appreciated in a successional context. Many man-aggravated stresses such as grazing, fire, and cultural

treatments in the forest can prevent some species from maximizing their potential on a given site. In other words, the large, encompassing concept of the dynamic forest community must be examined and appreciated before the regeneration of a single species can be examined.

The literature contains many views of succession in context of the forest. The following sections focus concepts of succession on the oak regeneration problem.

General succession

The distributions of organisms along environmental gradients typically form bell-shaped curves. The curves overlap broadly and vary independently of one another, indicating that each population has its own habitat requirements, width of habitat tolerance, and therefore, its own zone of maximal importance. Such continuous replacement of plant species along a gradient is called a vegetational continuum. The change in community composition over time is called succession (Pianka, 1983; Barbour et al., 1980; Drury and Nisbet, 1973). Succession is a pattern of change in the specific composition of a community after disturbance (Horn, 1974). Succession can also be defined as the process of development in an ecosystem, brought about primarily by the effect of organisms upon the environment and upon each

other, toward a relatively stable condition of equilibrium (McIntosh, 1981).

Secondary succession is the invasion of an area that has been previously occupied by vegetation (Barbour et al., 1980). Secondary succession is usually a result of interspecific competition between specifically adapted species (Horn, 1974). This review will deal exclusively with secondary succession as seen on forested sites.

All canopy layers in a forest undergo asynchronus composition changes with time (Grime, 1979). Succession will continue until an optimum species mix is established for a given site (Drury and Nisbet, 1973). Dynamic equilibrium will be reached when changes occurring in the stand are non-cumulative, random events fluctuating around a long-term mean (Barbour et al., 1980).

Succession is determined by the biological properties of the individual species. The rate of succession depends upon the ability of each species to regenerate itself and replace other species (Horn, 1981b). Succession can be slowed by a species regenerating itself. High self-replacement rates are found in quasi-stable states and the "final" stable state of a system (Horn, 1975a). Natural selection favors self-replacement (Horn, 1981b).

Evolution tends to slow successional convergence and eliminate any pressure of a species adapting to a given successional state. Successional states are the complex of species importance peaks along physical gradients, with boundaries sharpened by interspecific competition (Horn, 1981b). Both early- and late-successional species may invade a site simultaneously with differential growth rates, shade tolerance, and interference resulting in the surviving species-mix. The final state of succession is limited by the number of species available to fill potential niches. In areas that are species poor, there may be few late-succession species to develop a "climax" type. In high diversity areas, there will be a wider range of species for niche-filling (Etherington, 1982). Succession in productive habitats is a complex phenomenon reflecting relative dispersal efficiencies of plants and progressive modification of the soil and microclimate by the changing vegetation (Grime, 1979). The final stage of succession is a mosaic of patches of successionally different stages (Horn, 1975a).

Interactions with herbivores, predators, and pathogens are of critical importance in succession (Connell and Slatyer, 1977). Interaction of various site components with succession has been summarized in the following quote:

"Each vascular plant population is the basis of an allelochemic complex comprising the plants of that species, their consumers, symbiotic fungi and bacteria, and predators and parasites upon these species, or a component community ..." (Whittaker and Levin, 1977).

Within the techniques of study in succession, it is necessary in most theoretical work to assume a homology between a spacial sequence of vegetation at one time and a temporal sequence of vegetation on one site (Drury and Nisbet, 1973). In this study, the equality between the regeneration ecology over all sample areas and the regeneration ecology upon a single area over time is assumed.

Knowledge of the regenerative strategies of plants is particularly relevant to an understanding of successional and proclimax vegetation. A proclimax occurs in a region where disturbance, applied repeatedly in an orderly fashion, results in a characteristic vegetation type. When the intensity of disturbance fails to completely remove the vegetation, succession will tend to be arrested at some point where good interferers, best adapted to the disturbance, are the dominant species (Grime, 1979). Therefore, succession should be interpreted by physiological-ecological means and patterns, the results of

stochastic replacements under competitive interaction (Etherington, 1982).

The major problems in the modern landscape that are changing successional roles are: (1) the dissected and isolated islands of vegetation restricting species distribution, especially of late-successional species; (2) the intensively exploited landscapes becoming eutrophic due to the release of resources; and, (3) the arresting of succession at a competitive stage rather than the natural movement toward the biologically stressed situation (Grime, 1979). Eastern Iowa forests have these problems.

Concept of climax

The concept of climax assumes the physical environment remains constant, while changes in specific composition of the community become undetectably slow or cease altogether (Horn, 1981a). If significant changes in species composition do not occur in 500 years, the community is said to be at a climax (Barbour et al., 1980). Community stability can be defined as compositional changes remaining constant for 3-4 generations of the longest-lived species (Woods and Whittaker, 1981). Climatic climaxes may exist, but may not be a useful concept in areas that contain few dominants, occur far from glacial refugia, and have high frequency disturbances (Soloman et al., 1981).

There is some question as to whether a climax can exist. According to some, no sexually reproducing individuals in a community exist in steady-state equilibrium, and therefore, succession never stops (Connell and Slatyer, 1977). Individual climax communities are absent, and the steady-state is composed of a mosaic of unstable elements where succession and disturbance are balanced (Whittaker and Levin, 1977).

Incorporating the term "climax" into a forest mosaic causes the definitions to become altered. Climax then becomes a landscape with varying seral stages represented in a complex mosaic or pattern, continuously shifting (McIntosh, 1981). Each early-successional species should persist in the climax as long as there are dependable supplies of openings for invasion (Horn, 1974). If a climax community is disturbed, the return toward climax will be slowed if early-successional species efficiently reproduce themselves. Self-replacement, local seeding, and a low mortality rate among early-successional species will slow the transition to late-successional species (Horn, 1974).

Diversity of a climax community will be lower than that of some preceding stage. Diversity will be higher for intermediate disturbed communities (Horn, 1974). In other words, diversity increases throughout early succession, but

then decreases in late succession as a few species dominate the site (Barbour et al., 1980).

Stability

The concept of stability is found associated with succession, but few authors can agree on a definition. I do not believe stability is a useful term unless specifically defined within a given situation. Terms that may denote more clearly the concepts previously sought by invoking "stability" are resilience and inertia. Resilience, the ability to return to equlibrium, decreases with succession (Barbour et al., 1980). Inertia is resistance to change. Succession is marked by increasing inertia, by reduced dominance, and by increasing species diversity (Grime, 1979).

Stability of a community depends on the temporal and special distribution and the intensity of disturbance (Connell and Slatyer, 1977). Stability is also dependent on scale. A one-tree system is not stable, compared to a regional forest (Woods and Whittaker, 1981). The recovery of the steady-state position from even small disturbances will be slowed if each species reproduces locally in patches, instead of statistically over the entire site (Horn, 1981b). Aside from single-species forests with self-

replacement, the simplest base for stability would be a reciprocal replacement between two species. This replacement pattern requires an avoidance by the seedlings of one species for the space beneath its own canopy trees (Woods and Whittaker, 1981).

Production and development

After disturbance, development of the ecosystem passes through phases of reorganization, aggradation, transition, and steady-state (Figure 1). With sufficient time and a constant macro-environment, steady-state can be reached. A carbon balance is reached during the aggradation phase (i.e., input=output), and steady-state (i.e., living biomass stabilization) would occur later. In a strict sense, however, there can be no steady state, but a system undergoing slow, longterm changes. Additional disturbances can cause disorder in successional sequences that will modify development (Bormann and Likens, 1979).

In Figure 1, after disturbance, the standing crop of biomass declines through a reorganization phase. The biomass then increases to a maximum point through the aggradation phase. Biomass will erratically decline through a transition phase to approach a steady-state, where biomass is stabilized with irregular oscillations around a mean.

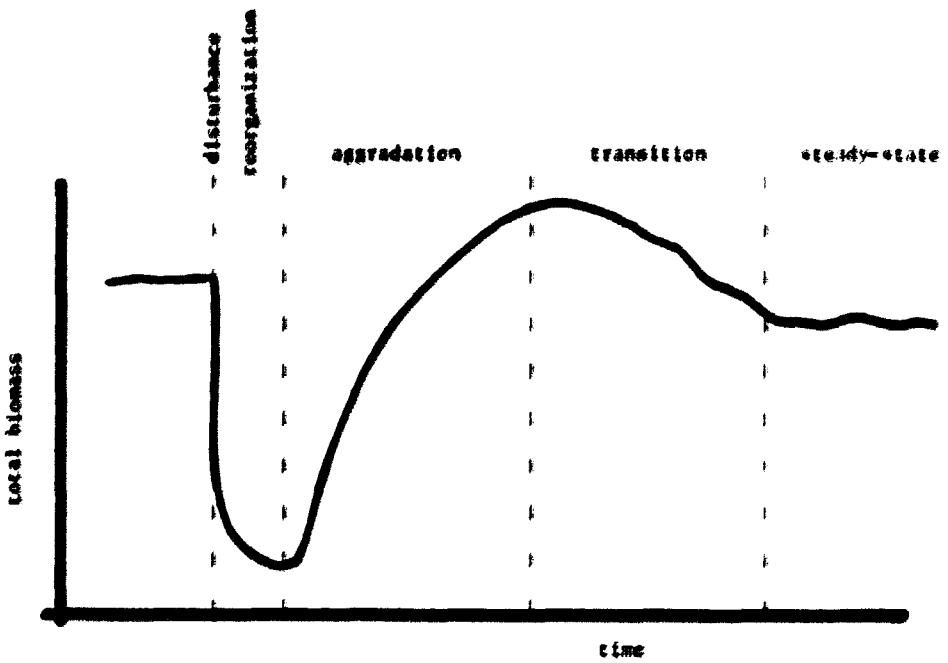

FIGURE 1. Ecosystem development after disturbance (Bormann and Likens, 1979)

This sequence reflects a shift from an initial even-aged condition to an all-aged condition (Bormann and Likens, 1979).

After disturbance and reorganization, production of structural materials increase steadily to a plateau dictated by site conditions. The rate at which this plateau is approached depends upon the initial rate of tree establishment. After the initial plateau, net production should drop gradually as non-photosynthetic biomass increases. The rate of drop depends on density and tree senescence. During this period of thinning, regeneration will be minimal. When thinning reaches a point where existing trees can no longer successfully preempt resources released by tree mortality, regeneration will resume (Peet, 1981).

The period of time that regeneration is interrupted will have a major impact on stand biomass and production (Peet, 1981). The lack of strong oak regeneration in the mature stands in eastern Iowa may stem from this problem of resource preemption. Once regeneration resumes, forest development will initially be dominated by establishment, but domination will quickly change to mortality. A balance between establishment and mortality will eventually be reached (Peet and Christensen, 1980).

Production exceeds respiration in early succession by an amount that accumulates as biomass (Horn, 1974). The period of initial establishment and canopy closure defines the recovery period for production. The buildup of biomass and associated inhibition of regeneration by established trees introduces a time-lag into the system roughly equivalent to the time period required for trees tc reach the end of major height growth. Established tree growth will compensate for tree mortality initially, but biomass and production will eventually drop on the site, and regeneration will resume, with new trees filling canopy gaps (Peet, 1981; Peet and Christensen, 1980). The end of the aggradation phase (i.e., dominance by old, even-aged trees) is a period of instability (Bormann and Likens, 1979). Additionally, new living material will start to use more synthesized resources than it produces. At this point, gross productivity will decline and respiration will increase until production equals respiration (Horn, 1974).

A special point of stand development should be made regarding natural thinning. Thinning usually has little affect on compositional changes because adult tree crowns move into any open space (Cottam, 1981). Thinning results in accelerated growth among on-site trees and usually no increase in recruitment. Canopy removal is required to

stimulate regeneration. Once natural thinning begins in a stand, a constant proportion of the population dies each year (Christensen and Peet, 1981). Areas of high density that were thinned never recover from initial density effects, as shown by high mortality rates continuing after release. Tree geometry, once fixed, can lead to problems later in the life of the stand and sustain the initial mortality rate (Peet and Christensen, 1980). Dense stands have a short period of resource availability, limiting the period for successful establishment. Thinning is more rapid in dense stands with degeneration of the initial species occurring earlier in the life of the stand. In poorly stocked stands, the period of resource availability is long, with the initial species on the site dominating longer. This allows more wind-dispersed species, as opposed to gravity-dispersed species, in early stand development (Christensen and Peet, 1981).

Early in succession, production should be high, due to a large pool of available nutrients. After the pool has been exhausted, production should be limited by nutrient inputs (Peet, 1981). Resource availability decreases in early stages of succession and is lowest in intermediate stands as biomass levels peak (Christensen and Peet, 1981). Maximum productivity and the tightest nutrient cycles are in

the central portion of a successional series (Peet and Christensen, 1980). High site quality leads to increased productivity, and this will accelerate natural thinning. The environmental fidelity of a species appears greatest when resources are the most limiting and interference is most intense, hence, during mid-succession (Christensen and Peet, 1981).

In a stand, if mature canopy trees are greatly disturbed, the understory stems will be released to compete for canopy dominance. Intense interference should follow with little reproduction possible. Slight canopy disturbances may allow increased tree regeneration while minimizing the understory growth that would take over the site with greater site disturbances (Peet and Christensen, 1980). If tree reproduction does not occur, the stand will progressively move from growth to thinning to senescence. If tree reproduction does occur and if seed dispersal is localized, a patchwork of reproduction will result, with abrupt distribution boundaries between patches on the poorer sites (Horn, 1981a).

Site disturbance

Succession can be dominated by a pattern of disturbance and/or by a stationary community. The domination balance is

controlled by a) the frequency of disturbance compared to the speed of convergence on a steady-state level; b) the number of different communities resulting from disturbance; and c) the persistence of disturbance effects (Horn, 1981b). The reaction of any system to disturbance is either an adjustment or a resistance. The process of succession represents an adjustment. If a community resists disturbance, there can be no succession (Connell and Slatyer, 1977). Since succession is the process by which a community recovers from disturbance, the more extensive and/or intense a disturbance, the poorer the chances are that the final composition will resemble the original composition (Connell and Slatyer, 1977). The pattern of recovery begins after a severe disturbance, with the site dominated by an establishment phase of compositional change and tree growth. After a short period of time, establishment is halted by the development of a dense stand. Forest succession then follows a thinning/mortality curve which lasts to the next disturbance. Natural thinning, in time, will create a mosaic of thinning and regenerating patches (Peet and Christensen, 1980).

If disturbance is synchronous and on a large scale, then it simultaneously ends the life of all trees, with the species best able to invade persisting until the next major

disturbance. This is the pattern in most forests (Horn, 1981a). Recruitment in large disturbed areas is less representative of the previous composition than in small disturbed areas. If the disturbance occurs at regular intervals, competitive advantage is held by early-successional species whose seed production periods are less than the disturbance period (Horn, 1981b). With no disturbance, canopy gaps are not frequent or sizable enough to allow for early-successional species to maintain canopy positions. Changes in disturbance frequency and intensity can allow gap-dependent species to be present in a stand (Doyle, 1981). Therefore, if the direct effects of disturbance are persistent, then understanding a forest community requires a knowledge of its history (Horn, 1981b).

Disturbance is considered endogenous if individual trees fail due to death by interference. Exogenous disturbance results from forces outside the developmental neighborhood that kill trees that were healthy before the event (Bormann and Likens, 1979). Endogenous disturbance is found predominantly in late-successional stands, and exogenous disturbance is the major cause of early-successional stands. One small, endogenous disturbance of a "climax" stand can lead to an off-centering of the system that may then develop toward a new stable-state (Horn,

1975a). The patterns found in the forest will be the cumulative effects of disturbance on communities (Coyle, 1981).

Conceptual successional types

A series of alternate approaches and formulations have been proposed for conceptualizing succession. Each proposal is not exclusive but may apply over specific successional sequences (Peet and Christensen, 1980). The continuum of succession runs between facilitation of compositional change by the current site occupant and the inhibition of compositional change by site occupancy (Connell and Slatyer, 1977; R. K. Peet, Department of Botany, University of North Carolina, Chapel Hill, North Carolina, personal communication, 1984).

The facilitation model of the succession states that later-successional species are dependent upon earlier species to prepare a favorable environment. This implies a high degree of community organization. This model has been found to be most adapted to primary succession situations (Connell and Slatyer, 1977).

The inhibition model of succession states that no species has a clear interference superiority over another. Whichever species colonizes the site first holds it until

death. After all available space is filled, invasion is only possible if the new species can survive with minimal resources. The species composition of a site will shift to those species that live longer. Late-successional species, as compared to early-successional species, have inherently longer life spans and are resistant to being damaged or eliminated by physical and biological factors. Once colonists secure the site, they inhibit invasion of subsequent colonists unless damaged or killed (when resources would be released) (Connell and Slatyer, 1977).

Between the two models of succession is the idea that succession leads to a community composed of species most efficient in exploiting resources, with each species having a highly differentiated niche space. In light-limited forests, later-successional species can invade only if they can grow with a lower level of light resources than early-successional species. Successional status is determined by differential species longevity, colonization success, and tolerance to interference. The species most tolerant of site conditions present will survive (Connell and Slatyer, 1977).

The inhibition successional patterns apply to most secondary successions and seem to apply to most forests in intermediate stages of development. Facilitation patterns

assume that only certain early-succession species are able to colonize a recently disturbed site, and therefore, acccunts for primary succession. A successional sequence may be brought about by disturbance, stress, species attributes, and associated shifts among those species whose niche hyperspace is optimal for the site. Research is still needed to determine the conceptual model(s) that best fit the patterning of the "real world". Interactions of species and the environment create synergisms and inhibitions that cannot be deduced simply by examining a species list (Cottam, 1981). Care should also be taken in simplifying life-histories, and in assuming spacial and temporal similarities in various communities.

The current model best suited, according to several authors, for describing successional functioning in forests is strictly the inhibition successional pattern. Early-successional species quickly secure space opened by disturbance and hold it by suppressing the establishment and growth of later-successional species. Even with greater light levels, late-successional species of trees can be suppressed by root competition. Later-successional species survive in a state of "suspended animation" until more resources are available. They accomplish this by having a lowered metabolic rate, repairing damage, and fending off

attacks of herbivores and pests (Connell and Slatyer, 1977). The effect of a species already in residence on the site delays, rather than facilitates, successional replacement. Interspecific competition permits one group of plants to temporarily suppress slower growing successors. Late-successional species are not out-competing early-successional species, but are filling in the spaces left vacant and preventing subsequent invasion by earlier species (Drury and Nisbet, 1973).

For example, establishment of tree seedlings can be inhibited by interfering herbs which, because of their lateral spread above and below ground, are better equipped to dominate the understory in the short run (Grime, 1979). After a severe disturbance, or a short respite from continuous disturbance, there is usually a burst of regeneration that suppresses later regeneration, thereby providing a single age-class that may dominate the site for long periods (Connell and Slatyer, 1977). Invasion and establishment during succession are episodic due to resource availability patterns (Christensen and Peet, 1981). Regeneration will not occur, even in the abundance of one resource, if other resources are preempted from use.

Species characteristics

The principal species factors determining successional status are longevity, tolerance for reproduction in an occupied environment, and dispersibility (Whittaker and Levin, 1977). With time, succession slows because of an increasing scarcity of conditions suitable for seedling establishment and the low seed production and dispersal rates associated with late-successional species. Most trees are generally stress-tolerant competitors, with the vegetation causing progressively more stress in succession (Grime, 1979).

The single most critically limited resource throughout succession is light. The optimal leaf arrangement for intercepting and utilizing light most efficiently is a function of the light incident on the tree. At light levels above 25% of full sunlight, the leaf is functioning at greater than 90% of its potential photosynthetic rate. To optimize energy input at lower light levels, the tree must intercept all available light present. The form of optimization is a monolayer of leaves around the outside of the canopy where leaf area index (LAI) is approximately one. At high light intensities, the tree can optimize leaf distribution, and therefore, energy input, by having leaves throughout its total branch volume. The light quality and

quantity constraint mechanism in a leaf leading to energy optimilization is the balance between respiration and photosynthesis (Horn, 1975a).

Leaves generally require at least 2% of full sun to maintain a positive carbon balance and to kept on the tree. In the open, a monolayered tree with a smaller LAI cannot compete with a multilayered tree. In deep shade, growth of multilayered trees is curtailed because interior leaves must import assimulated carbon for survival. A monolayered tree produces dense foliage at the tips of well-lighted branches. A multilayered tree produces more lobed foliage at the tips of well-lighted branches and at the tips of any interior branches that produced excess sugars in the previous year (Horn, 1975a). The optimization of light capturing systems can determine successional status of trees.

In a multilayered-crown tree, sensible heat and transpiration are spread over a larger leaf area, compared with a monolayered-crown tree. Water use efficiency (the ratio of carbon dioxide taken up to the amount of water transpired) is greater for a multilayered tree than for a monolayered tree. The canopy of undisturbed forests, where monolayered trees dominate, will exhibit little or no new growth (i.e., senile) (Horn, 1975a) but still transpire large volumes of water.

Multilayered trees are able to grow faster than monolayered trees on the open sites of early-succession. Shaded understory areas of multilayered species are less suitable for auto-replacement than for monolayered species. As monolayered species reach the canopy, regeneration, if present, will be with monolayered species. Multilayered species will survive best in larger gaps or openings. Wood production will drop in time because monolayered trees are less productive than the multilayered trees they displace. Successional changes will lead to the most aggressive species of nonclayered tree completely eliminating its competitors, given that time and site are not limiting (Horn, 1975a).

Site factors

The major environmental factor affecting succession is climate. Climate exerts the ultimate control on forest associations. Use of simulations have shown that small climatic changes (0.5 degrees Celsius in annual mean temperature) can affect the dominant species present on a site (Woods and Whittaker, 1981). Changes in degree-days can have a great effect on species frequency. Small degree-day changes (i.e., 250 degree-days per year) can cause abrupt species changes. Species changes also depend upon

whether degree-days are increasing or decreasing, i.e., a hysteresis effect (Shugart et al., 1981; Prubaker, 1981).

In hardwoods, soil moisture conditions and cation availability (Ca, Mg, pH) were found to be highly correlated with vegetational variation (Christensen and Peet, 1981; Horn, 1975a). With succession, the major site of nutrient storage shifts from the soil to the plant biomass. Litter becomes a major nutrient compartment (Barbour et al., 1980). Nutrient immobilization (nutrient stress) occurs in late succession by compartmentalization of nutrients in standing biomass and in accumulated litter. Nutrients are also immobilized due to the faster recycling of carbon compared with other elements in the litter, which causes an increasing level of nutrient limitation on growth (Etherington, 1982). As the biomass on a site reaches an equilibrium point, (carbon loss = carbon gain), nutrient loss from that biomass will increase due to material turnover. The change of relative nutrient levels at this time may lead to changes in species composition.

A tree will influence its site for a long period of time. The influence includes the amount of time the tree is living, the time spent as a dead snag, and the time when interacting on the forest floor (Cottam, 1981). One tree can influence a site for thousands of years depending upon

its species, size, and site location. The influence of a tree that stood on a site may affect species composition for many years.

Root succession

In the forest, most energy consumption, energy transformations, and elemental transformations occur below-ground. Above-ground patterns in the vegetation of the forest will be indicative of major changes below-ground (Cromack, 1981). Little work has been done with successional patterning below ground. The below-ground portion of the forest includes: a) plant roots and associated microflora; b) heterotrophic microorganisms and soil animals; c) bacteria specialized in elemental transformations (i.e., N, S, Fe, Mn); d) pathogenic or parasitic organisms; e) organic matter; and f) mineral soil (Cromack, 1981). Each component is dynamic and will interact to a greater or lesser degree with other components of the community, thereby causing complex changes to occur in total underground community dynamics.

Significant changes in below-ground community activity are associated with major forest disturbances. Root death is a major contributor to soil organic matter, even exceeding above ground litter fall. Litter and fine, live

roots, especially of early-successional species, decay rapidly, causing rapid turnover of material. Soil animals chemically and physically alter organic matter and litter. Fungi in the soil exploit pore space while bacteria colonize solid surfaces, including dead fungal hyphae. Each organism is highly differentiated and may follow the same general successional trends as above-ground organisms. The below-ground complexity is staggering and should not be underestimated (Cromack, 1981).

It should be noted that when the term "root" is used here in a forest context, the definition includes the mycorihzal fungii, the tree root, and in a general sense, the rhizosphere. The tree rhizosphere is the environmentally interacting area of the soil-held plant portions. Generally, the plant root and the associated mutualistic fungii (in total = mycorihzae) can comprise the dominant symplast/apoplast boundary between the tree and its environment.

Forest history and species migration

To place succession in a historical context, a simple review of the fossil/pollen record is needed. During the Quaternary geologic time period, forests seldom maintained a constant species composition for more than 2000 to 3000

years at a time. Forest communities are chance combinations of species, without an evolutionary history of their own (Brubaker, 1981; Davis, 1981). In eastern North America, many tree species that occur in the same stands today did not grow together in the past, and vice versa. Many north-temperate forest communities did not exist 20,000 years ago. Environmental and competitive interactions have changed too rapidly to permit close co-evolutionary relationships to develop. Trees interact in general ways with each other, and therefore, appear as loose associations which change through time (Brubaker, 1981). Fine adjustments of species to one another may have occurred as a result of evolution, but the species must have also co-occurred long enough for adjustments to take place (Davis, 1981).

Many species have not been in climatic equilibrium since the last glaciation (14,000 years ago), therefore, climax theory seems refuted. However, in refugia of species during glacial periods, and now afterwards, climax associations may exist. Differential species migration rates away from glacial refugia cause vegetation changes that are out of phase with climate change as distance from the glacial refugia increases (Brubaker, 1981). In other words, the speed with which a forest can adjust to climate is far exceeded by the speed of climatic change (Davis,

1981). Also, if climate-related factcrs strongly affect seed germination and juvenile tree acrtality rates, pre-twentieth century conditions may have been acre important than recent conditions in determining present species composition on a site. Changes of 250 growing degree-days (GDD - 50 degree Fahrenheit basis) have been shown to completely eliminate a species frcm a site in Tennessee (Solomon et al., 1981). GDD has increased 500 units in the last century on the basis of Toronto data (Brubaker, 1981).

Seed availability ultimately controls the migration of a species, not the increasing temperature in the receding path of glaciation. Migration was not a linear front in sany species, but extended in particular directions on the basis of physical, biological, and environmental characters (Table 1). Some species moved faster than others, but seed dispersal was not the sole explanation cf the rapid movement. The survival/persistence atility of invading species may be the most important factor permitting spread. An example from pollen records is the rapid movement of large seeded Quercus and Carya spp., with less rapid movement cf lighter seeded species. Another interesting point is the great importance American hornbeam (Carpinus caroliniana) must have played in early species-poor forests since its pollen record is of great magnitude (Davis, 1981).

TABLE 1. Average rates of Holocene range extension and time of first arrival in Iowa for four tree species (Davis, 1981)

species	range extension rate (m/year)	first arrival (years before present)
oak	350	10,000
elm	250	11,000
hickory	225	10,000
maple	200	11,000

Microsites

A vascular plant occupies a definite place on the ground (below which it is rooted and above which foliage is borne), called a microsite (Whittaker and Levin, 1977). The presence of the plant defines the microsite. Microsite size increases as the plant grows, with increases in plant size suppressing other competing seedlings in their microsites. With plant death, numerous microsites may become available for other seedlings. A mosaic of microsites with different physical properties will contain a mix of species adapted to specific microsites. Each species will then superimpose its own allelochemic, competitive, and physical effects on the site (Whittaker and Levin, 1977).

A dynamic equilibrium exists between vacant and occupied microsites. Population survival depends upon changes in the dispersal density of seeds and seedlings,

survival to reproduction age, and replacement of adults lost by death (Whittaker and Levin, 1977). Interactions between species take the form of a race for unchallenged dominance in recent openings, rather than direct competition. An individual of any species may die and be replaced by an individual of any species (Horn, 1981b). The reproductive fate of a given spot in the forest is dependent only on the current occupant and a limited number of neighbors. This suggests that tree-by-tree replacement processes are reasonable approximations of "real" processes (Horn, 1975a).

Effects of canopy species on reproductive microsites seem particularly important in maintaining both compositional stability and diversity of forest communities (Woods and Whittaker, 1981). The development of individual plants or a vegetation canopy will substantially modify the local environment and microsite (Etherington, 1982). An invading species will be represented by many seedlings, fewer saplings, and several small trees. Locally reproducing species will have trees in several age classes, with a large number of young trees. A stand containing only older trees is senile, and can continue only if the present trees reproduce sufficiently to replace dead and dying trees. If not, invading species will begin to dominate regeneration sites (Horn, 1975a). This latter event may be

similar to the sugar maple invasion of mature oak stands in eastern Iowa.

The number of microsites determine whether succession will be predominantly by species dominance of the site or by randomness and accidents of history (Horn, 1981a). Major disturbances, senescence, suppression, pests, herbivores, and the falling of other trees are the principal elements causing tree death and gap occurrence (Doyle, 1981). Gap size needed for regeneration vary between species. Important differences in species requirements for gaps (microsites) will be most magnified at the seedling level with light-tolerant species able to become established in relatively smaller gaps than less light-tolerant species. The early stages of the life cycle will be the most important from the standpoint of community dynamics (Woods and Whittaker, 1981).

When proper microsites are sparce, the forest is a patchwork of evenly-aged cohorts near parental trees, with intervening areas filled with a mixture of species and ages. When proper microsites are sufficiently abundant, the forest will be first dominated by rapidly growing, shade-intolerant trees, some of which will have persisted from the start of succession, and some which have invaded. If the presence of vigorous young plants is strongly dependent on nearness to

mature plants, or a highly seasonal rain of seeds, succession will not converge but will remain a patchwork of different species cells (Horn, 1981a and b).

Microsites, without a tree stem present to provide a physical location, are continuous with one another and are not discreet, countable units, but rather a general measure of the maximum packing limit possible for reproduction of a species. Stabilization of microsite equilibriums could be produced by "perfect" undifferentiated microsites. Since microsites are not perfect and do differ in some qualities, species growth and development will differ over the microsites supporting that species. If microsites differ in numerous characters, each character may act as an axis delimiting a hyperspace in which all possible microsites are presented, and along which the character or variable levels are distributed. Each species will occupy a specific portion of this hyperspace and will evolve at different rates toward different portions of the hyperspace. Differentiation of microsites provides for the co-existence of a number of species (Whittaker and Levin, 1977).

Dispersion of species around their mean values in a microsite hyperspace varies over time. Variance in hyperspace positioning can describe species behavior differences in response to fluctuations along each axis or

gradient (Whittaker and Levin, 1977). A niche space (i.e., acceptable microsite type) of a species can be defined by the axes of biological factors within the canopy and roots, by soil and topography substrate factors, and by gap factors such as size and age (Woods and Whittaker, 1981). Each population is regulated by a multi-component microsite pattern in space and time (Whittaker and Levin, 1977). The ecological/physiological limit on a species is its niche size relative to available microsites and the amount of niche overlap with other species.

A species can invade a site when the ratio of its colonization of new openings to its death rate is higher than that of the current monopolist of the site (Horn, 1975b). When some portion of the microsites in an area are unoccupied at any time, two or more species can persist within the area in a steady-state. Once a microsite is occupied by either species, other seedlings of both species are suppressed. Microsites must be occupied with enough seedlings of each species to replace mortality (Whittaker and Levin, 1977).

Any compositional equilibrium will drift randomly in time. Site equilibriums can be stabilized if one species can only survive in microsites abandoned by the other species or in microsites adjacent to those occupied by

others. This allows a competitive advantage to rare individuals isolated in their own neighborhoods from others of their own species, due to lack of intraspecific competition (Whittaker and Levin, 1977). The greater the migration rates within the forest, the fewer microsites that will be unoccupied at equilibrium. This will cause more direct interference between species than just occupation of space. Greater migration rates between microsites tend to smooth out patchiness and produce interference limits to increases in diversity (Horn, 1974).

Trees may occur in evenly aged groups dating from episodes that favored seedling establishment. Much of the patchiness of regeneration is a function of the probabilistic accidents on the site at a given time (Horn, 1981b). Random replacement can account for the observed replacement frequencies, except in cases of vegetative reproduction (Barden, 1980). Colonization of a site by a species depends on its presence, not necessarily on its abundance (Horn, 1981b). Early invasion is not a prerequisite for eventual colonization (i.e., oak and hickory are invaders), and early establishment is no guarantee of success (Christensen and Peet, 1981). Tree reproduction in temperate forests tend to avoid growing under members of their own species. Seedlings of a species

may have a greater probability of surviving when their roots are interfering with roots of another species, rather than when their roots are subject to the more intense interference (and grafting) with the same species (Whittaker and Levin, 1977).

Each regenerating patch in the forest originates as a canopy gap formed by a localized disturbance, with the degree of patchiness reflecting the magnitude and periodicity of the disturbances (Boyle, 1981). Gaps must be large enough to provide space for root colonization and proper conditions for mineralization of soil nutrients (Gomez-Pompa and Vazquez-Yanes, 1981). When a gap is formed, mature trees laterally expand into the area at a rate of 4 to 8 cm per year (Bazden, 1980). Gap dynamics can also be changed by the species involved. For example, some species die upright and stand for many years while other species die and quickly fall (Woods & Whittaker, 1981). Each species will produce a different type of gap. The larger the trees become, the greater the gaps left by their fall, and the greater the chance for early-successional species to invade (Gomez-Pompa and Vazquez-Yanes, 1981). Large crowned, shade-tolerant trees are replaced by small crowned, gap-phase species that are, in turn, replaced by shade-tolerant species (Woods and Whittaker, 1981).

Gaps larger than that produced from an individual tree loss are infrequent, but do offer early-successional species space inside late-successional forests when they do occur (Barden, 1980). The abundance of early-successional species will depend upon the frequency of openings in the canopy that allow direct sunlight to strike the forest floor (Gomez-Pompa and Vazquez-Yanes, 1981). Early-successional species are short-lived and must be replaced more often on a site than longer-lived, late-successional species (Connell and Slatyer, 1977). The larger the number of replacements, the quicker the species can be removed from the site, assuming removal is the expected fate of the species. Dominance of shade-tolerant species in the forest indicates that small gap replacements by saplings is the normal means of tree replacement (Woods and Whittaker, 1981).

Specific methods of modelling succession

This section briefly reviews several of the major methods, as opposed to the earlier discussion of basic successional concepts, for modelling succession. There are four major successional modelling methods found in the literature (Peet and Christensen, 1980):

1) Life history--Succession is pictured as a gradient along which species are displaced by competition. Prediction of change involves identifying a number of "vital attributes" of each species (e.g., Noble and Slatyer, 1977; Cattelino et al., 1979; Gomez-Pompa and Vazquez-Yanes, 1981).

2) Differential longevity--Succession is a visible end-product of differences in longevity. Dominants enter a community early in development when competition is less. Initial site conditions and species composition will determine the stand composition. Failure of a species to become established early reduces or prevents eventual dominance (e.g., Drury and Nisbet, 1973).

3) Stochastic process--Probabilities of tree replacement are computed and applied on a tree-by-tree basis. A statistical consequence of this formulation is usually a convergence to a steady-state condition. This process can also be used on various higher-order tree groupings. Two subdivisions within this group exist: stand models of tree-by-tree replacement (e.g., Shugart et al., 1981; Ecyle, 1981; Solomon et al., 1981); and Markovian models (e.g., Horn, 1981a, b; Horn, 1975a, b).

4) Population process--Variation in rates of reproduction, establishment, growth, and mortality control succession.

Trees become segregated in forests along gradients of moisture availability, soil fertility, and disturbance history. Seed dispersal and proximity to seed sources determine stand composition. Species life-history and physiological characteristics help determine population changes relative to environmental changes. Population processes influence species composition, rates of change, diversity, productivity, and biomass (e.g., Peet and Christensen, 1980; Christensen and Peet, 1981).

Descriptions of the separate work on each successional research area is beyond the scope of this review. Only Henry Horn's work will be briefly highlighted, since it provides a background for modelling work later in this dissertation.

The core of Horn's succession models are Markov chains. A Markov chain is a stochastic process in which transitions among various states occur by specific probabilities that depend only on the current state of the system and not any previous state (Horn, 1975b). A Markov successional process is where each tree has a certain probability of being replaced by another of its own kind or by another species (Horn, 1974). The tree-by-tree replacement model, using Markovian matrix treatments, assumes that knowledge of a species occupying a given spot may narrow the statistical

range of likely occupants of that spot in the near future. The model also accepts that replacement probabilities depend only upon what species occupies a given spot and do not change unless the occupant changes (Horn, 1981a). This technique can be utilized under the inhibition conceptual successional model.

Additional assumptions concerning species replacement by Markovian methods are: a) the forest is a honeycomb of independent cells, each occupied by a tree; b) each tree is replaced with a tree from its own understory; and c) the probability that a given species will replace another species is proportional to the number of saplings of the former in the understory of the latter (Horn, 1975b).

To estimate the probability of a tree species remaining in the stand after a period of time, the number of saplings of each species under a canopy tree is counted. A matrix of probabilities is then produced for that forest, assuming that every sapling under a canopy tree has an equal chance of replacing that tree (Horn, 1975a). Replacement probabilities are assumed not to change with time (Horn, 1981b).

The Markovian replacement process requires the multiplication of a row matrix (current forest canopy composition) by a square matrix (tree replacement

probabilities) for each time period. A single, stable end-point will eventually be reached (Horn, 1981b). After several generations (several multiplications of matrices), the abundances of species settle down to a stationary distribution, assuming the generations of each species is synchronous, which is an incorrect assumption and requires a correction factor for differential longevity of canopy species. If the stationary distribution is weighted by the longevity of each species, the actual distribution of species can be approached. Successive multiplications by a given replacement matrix cause a convergence on a stationary-composition stand. The convergence is not a biological consequence of succession, but a statistical one on the basis of the structure of the replacement matrix (Horn, 1981a).

A paper by Harden (1980) contains a replacement matrix for a cove site and a comment on the use of Markov chains. Harden stated that Markovian analysis assumes equal growth rates among species, and therefore, early-successional species that grow fast may capture more of the canopy than their density would indicate. Early invaders were also felt to affect subsequent replacement probabilities in complex ways (Christensen and Peet, 1981). In a 1980 paper, the same authors felt that Markovian models do not allow changes

in rates of replacement over time, thus making them less sensitive to short-term succession (Peet and Christensen, 1980).

Oak Regeneration

Introduction

The literature concerning oak regeneration in the central states is varied, extensive, and often quite old. Since the oak-hickory forest type is the most extensive of hardwood forest types in North America (Burns, 1983), the voluminous work on oak is not unexpected. What was unexpected from the literature was the relatively small number of researchers that have continued to work with oak regeneration. A handful of researchers in the central hardwoods region have produced many of the publications available. The data base of this past research is a tremendous bank of information. After reviewing the available information, it became clear that there were several schools of thought each revolving around an individual or a group of workers, and each having a particular approach and conceptual view of the oak regeneration problem. This literature review section will highlight the major problem areas and solutions cited within

the oak regeneration subject area and bring forward papers that contain closely allied areas of information felt to be critical for regenerating oak in the central states. The special cultural procedures associated with oak forest silviculture will also be reviewed, as well as several new silvicultural techniques that may maximize the potential for regenerating oak in eastern Iowa.

None of the known regeneration methods maintain or increase the amount of oak in a stand (Tubbs, 1977a). Information for developing continually successful oak regeneration systems is not currently available (Sander, 1978). The oak regeneration problem has been more complex than anticipated. The solution does not lie with simple protection of the woodlands from grazing and fire. The solution is also not found in textbook silviculture. To resolve the problem, reliance on the preconceived notions of what procedures comprise good silviculture must be eliminated. The six areas needing further research within the problem area of oak regeneration are the role of advanced regeneration, survival of the acorn crop, the role of fire, the role of allelopathy, the economics of light in the understory, and the role of artificial regeneration (Merritt, 1979).

Historical and successional trends

Before the last glaciation period (Wisconsin), the red oaks had a range as extensive as the present range. During the glaciation periods, the oaks were in refugia at least 80-160 km south of the ice sheets. With melting of the ice sheets, the oaks moved straight north into Iowa from the south (Schlarbaum et al., 1982).

Moving forward in time a number of millenia, early land surveyors called the oak forests of eastern Iowa "scattering timber" because of the relatively large distances between trees and the presence of an open prairie-type understory (Arend and Scholz, 1969). Current oak stands were thought to have developed from heavy cutting, grazing, and fire. With the present elimination of these stress/disturbance factors by landowners and society, foresters have been ignoring critical basic ecological relationships. On good sites, without fire and grazing, the natural processes lead toward the more mesic climaxes. Oak is then, by default, relegated to only the drier sites (Merritt, 1979).

To gain an appreciation of regeneration in an oak stand over time, an eighty-year-old stand of red oak in Wisconsin was examined. Most oaks developed under canopy gaps less than 150 square meters in size. Oaks were present as advanced reproduction throughout the stand. Oaks did not

survive beneath a closed canopy but did well under canopy gaps and beneath residual trees left after cutting. Oaks were found to develop well under partial canopies. The reduction of basal area by 49% stimulated oak seedling growth. If the oak reproduction was not beneath a very small gap, or overtopped by other vegetation, survival chances were good. Competition was modelled by measuring the distance to a competitor (interferer) and the relative height of the oak stem. The closer the interfering individual, the taller the oak needed to be for success (Lorimer, 1983).

Mature oak stands were found to be uneven-aged as though developed from a series of cuts spanning 20-30 years (Lorimer, 1983). Many stands are missing regeneration age groups from 1931 to 1941, possibly because of drought and livestock-feed shortages. Forest land has been intensively grazed, and that grazing attitude has continued (Auclair and Cottam, 1971).

The succession trend of the oak forests in this region is toward sugar maple "climaxes" on good sites. Black cherry in this area is considered an opportunist and can dominate a site. Hickories enter the stands when areas are opened by thinning. Even-aged stands are not expected to regenerate oaks for hundreds of years due to intense

interference. White oak, hickory, and cherry are cited as forming a stable community in the driftless area maintained by gap-phase replacement. When principal component analysis was used to delineate the forest types in the area, the two major gradients along which the stands were distributed were a moisture-nutrient gradient and a competitive tolerance gradient (Peet and Loucks, 1977).

In southern Wisconsin, the occurrence of late successional species beneath earlier successional species was not considered a successional movement. Instead, a stable situation was in place that was resource dependent. The site quality and photosynthetic array controlled the stability of compositional change on the site. Moist sites will tend to develop monolayer photosynthetic arrays. With movement along the moisture gradient to drier sites, a development of more multilayer communities will occur where the multilayer photosynthetic arrays include the shrub and tree canopies (Aber et al., 1982).

In the driftless area, only a few species ever reach high levels of importance in a stand, where importance is the number of stems on a per area basis. Most species will never occur highly important in any stand. In order of importance, red oak, sugar maple, and to a lesser degree, white oak were the dominants in the region. Tree species

seemed to occur along a gradient with much overlapping of importances in various stands. The idea that the species were occurring in the stands along a continuum or gradient supports the works of Gleason (1927 and 1939). The gradients along which the major tree species grew were a continuously shifting series of site character combinations with a definite sequence or pattern resulting from the limited number of species available over a range of sites (Curtiss and McIntosh, 1951).

Oak forests in New Jersey were found to have and maintain a constant number of seedlings, saplings, and mature trees. The steady-state form of the system had little numeric change, but species composition in each group were found to be quite dynamic (Good and Good, 1972). It is not known if eastern Iowa forests have this property.

Using a compositional change model with outside validation checks, it was found there was no single unidirectional trend in composition, but many trends in mixed hardwood forests. The oaks, with larger crowns, tend to dominate over smaller crowned species (Stout et al., 1975). Control of site resources would seem to play an important role in regulating compositional shifts.

Site quality

Within the oak forest, the successional trend is toward more shade-tolerant species especially accute on better quality sites. On poorer sites, less tolerant species predominate because of site limitations on growth and/or regeneration. Generally, oaks are found on drier sites where stands are more open and development of the shade-tolerant species is restricted (Sander et al., 1983). The species composition of a stand and its growth have been found to be most effected by soil moisture and climate (Arend and Scholz, 1969).

The reduction in light intensity in oak stands is great. Approximately 90% of the light intensity is lost in passing through the canopy. Another 7% of the light intensity is lost passing the secondary canopies of the suppressed trees and saplings. The final 3% of light intensity is lost in passing the seedling and shrub layer. The remaining light intensity is negligible at the ground level in denser stands, and individuals must grow in height in order to gain light resources. Regeneration is not occurring in ordered successional patterns, but primarily as a result of disturbance, successful colonization, and capture of the light resource (Auclair and Cottam, 1971).

In Missouri, the spectral quality of light (400-700 nm.) was examined over three different oak basal areas. All stands, regardless of basal area, were found to be similar in light quality, but the basal areas were found to be inversely proportional to light quantity (Garrett et al., 1977).

Dense overstories tend to favor herbaceous plants and inhibit woody plants, and therefore, regeneration of tree species. Partial shade may assist in getting the seedlings established, but full sunlight will be needed for maximum growth and the ability to interfere with other species on the site (Tubbs, 1977b).

Flowering and fruiting

The monoecious flowers of the oak genus are produced during leaf expansion in early spring. The oaks have the male flowers borne on ephemeral catkins and female flowers borne on stocks in the leaf axils of current year shoots. The acorn is the sexual reproduction unit of the oak family (Sander et al., 1983; Arend and Scholz, 1969). There are usually large numbers of male and female flowers produced every year. Seed crops though, as compared to flower crops, appear sporadic and infrequently (Watt, 1979).

Pollen production is usually great. Relative humidity is a critical factor for successful dispersion. Relative humidity must be below 45% for the anthers to open properly. If the air is too dry, the anthers will split prematurely. If the air is too moist, the pollen does not disperse and the male catkins will fall to the ground after a week or two, taking with them the pollen crop. Pollen shedding usually occurs over only a 3-4 day period, so other climatic factors can also effect the pollen crop (Watt, 1979).

Flowering in oak is innate, but acorn set and development are induced by the environment. A climatic pattern found to induce good female flower set does not have late spring frosts but does have rapid spring warm-up followed by cool temperatures into May. When mean daily temperatures steadily rise from early spring to June, acorn crops are usually poor. Mean daily temperatures need to rise rapidly in early spring so the leaves and flowers can expand early and develope fast. Warm temperatures of early spring advance catkin emergence and shoot development. Cool temperatures are then needed to insure proper reproductive organ development (Arend and Scholz, 1969; Sharp and Sprague, 1967). The cool periods following the warm spring temperatures, delay pollen dispersal to coincide with pistillate flower development. Heavy frosts during

flowering or early development can destroy the current years reproductive potential (Arend and Schelz, 1969; Watt, 1979). In only 15% of the years did frosts affect acorn yields in Wisconsin (Sharp and Sprague, 1967).

In years of heavy acorn crops, all acorns on a stock will develop. Usually, only one acorn develops on a stock and the rest die (Sharp and Sprague, 1967). Approximately 70% of the female flowers fail to produce an acorn (Feret et al., 1982). The female flowers and the acorns in the axils of lower leaves form abscission layers and drop off early in the season (Sharp and Sprague, 1967). This common occurrance of premature abscission of acorns was found to be 50% completed 30 days after pollination (Feret et al., 1982).

Upon pollination of the female flower, pollen tube germination and growth differ between the white oak group (Leucobalanus) and the red oak group (Erythrobalanus). In the white oak group, the pollen tube will grow into the ovary and ovule, and fertilize the egg in late June. In the red oak group, the pollen tube stops growing when it reaches the base of the style. The following spring, growth resumes and fertilization occurs in mid-June (Watt, 1979).

The white oak acorns mature by September and drop to the ground where germination occurs immediately with only

the radicle emerging. Acorns of red oak mature in 18 months from successful pollination, then fall to the ground and lie dormant until the next spring. Red oak acorns are exposed for a much longer period of time to pests and the climate/microclimate effects of the site than are white oak acorns (Arend and Scholz, 1969).

Oaks will start to produce acorns between 20-30 years of age, with the period of good production occurring after 50-70 years. Acorn production is positively correlated with DBH increases up to approximately 20 inches. Crown class, or the amount of direct sunlight reaching the crown will determine acorn yields. The more direct sunlight that strikes the crown, the greater the expected yield of acorns. Acorns will be produced only on branches that receive direct sunlight (Sharp and Sprague, 1967). White oaks will usually produce 66% as many acorns as the red oaks (Arend and Scholz, 1969).

Wind, precipitation, relative humidity, and vapor pressure deficits were found to not significantly influence acorn yields. Drought was also found to not reduce acorn crops in white oak (Sharp and Sprague, 1967).

The frequency and size of acorn crops are specific to each individual tree based upon species, crown size, exposure to light, and climate/microclimate factors. Some

trees will bear every year, while others will yield only a few acorns periodically. On a stand-wide basis, some acorns are produced every year (Arend and Scholz, 1969). Within a stand, the individual stems will range from having high fruiting potentials to low fruiting potentials (Sharp and Sprague, 1967).

Smaller crown trees will produce few good acorn crops. Increasing the crown size of an individual by thinning will not enhance acorn crops in all trees, but will increase the crops of the normally good seed-crop producers (Sharp and Sprague, 1967). Partial girdling of the tree to increase acorn crops is ineffective (Arend and Scholz, 1969).

The seed crop size of oak will vary from year to year. Comparing average sugar maple and red oak seed crops, the sugar maple has 61-100% of a full seed crop approximately every 2 years while having a 36% or less of a full seed crop every 2 years. Sugar maple can be expected to have a good to excellent crop every other year. Red oak has a 61-100% of a full seed crop every three years and a 36% or less of full seed crop every 2 years. Red oak is less predictable in seeding and has more poor seed years than sugar maple (Godman and Mattson, 1976). White oaks will produce a good male flower crop every year with good female flower crops produced in alternate years (Watt, 1979). To predict the

size of the fall-maturing oak seed crops, a tree with spring-maturing seeds might be used as a indicator species to estimate seed yields (Godman and Mattson, 1976).

In studies in New York and Pennsylvania, seed crops of white ash and sugar maple were found to be quite predictable from spring flower crops. The total seed yield differences found between oak trees related more to crown size, not the density of the flowers or of the seeds on a branch. Seed production was inversely correlated to stand density in red oak. White oaks were found to either have very good or very bad seed crops, while red oak showed that some trees were consistently good producers and some were consistently bad producers (Grisez, 1975).

Prediction of a good acorn crop is difficult to do more than a few months ahead of time (Sharp and Sprague, 1967). Visually estimating the acorn crop yield may be practical for crop forecasting. Red oak acorns hang below the associated leaf level, and therefore, can be counted from below the crown. White oak acorns are positioned above the general leaf level, so counting must be from outside the crown edge. The acorn counts should be the averages of the number of acorns on the terminal 24 inches of 20-30 upper branches. For red oak, a mean of 17-24 acorns per branch terminal is considered a good yield while 4-8 acorns per

terminal is a poor crop. In white oaks, good acorn crops are when a mean of 13-18 acorns is present per branch terminal with means of 3-6 acorns per branch terminal comprising a poor yield (Grisez, 1975).

A method of determining the number of acorns produced per square meter of ground surface from white oaks in Virginia was to estimate the number a peduncles per shoot. This value, multiplied by the constant 76.02, produced the acorn yield value. The coefficient of determination for the regression was 0.84. The yields estimated in good years were greater than 190 acorns per square meter beneath the drip line of the tree, and in bad years, there were less than 5 acorns per square meter beneath the drip line (Feret et al., 1982).

If acorn yields on sites with various levels of oak regeneration are compared, large seedling populations were not found to be related to the acorn crop sizes in the past. The amount of reproduction on a site is more a function of the site factors acting upon the acorn after falling off the tree and/or on the survival of the seedlings. Sound white oak acorns are more successful at producing a seedling than sound red oak acorns. The hypothesized reason is that early germination of white oak acorns minimized water desiccation, which is a known source of red oak acorn viability loss (Carvell, 1979).

Acorns tend to fall before the leaves, so a litter cover is common (Watt, 1979). If the acorn is not covered by litter, acorn germination and establishment can be inhibited by the failure of the radicle to penetrate the leaf mat. The acorn then succumbs to the environment due to the low moisture levels and high temperatures developed on the exposed litter surfaces (Tubbs, 1977b).

The ideal seedbed for successful acorn germination and development is a continually moist, well-drained, mineral soil protected by some litter. Germination and first year survival are best when the acorns are buried individually about 1 inch (2.54 cm) deep in mineral soil. Most seedlings come from acorns buried in, or in contact with, the mineral soil. Litter depths greater than several inches decreased the number of stems of reproduction due to a physical prevention of the radicles reaching mineral soil before desiccation (Sander et al., 1983; Sander, 1979).

Oak seedlings are found where the soil and litter has been disturbed. Oaks are also found to develop on sparsely covered grassy spots. Partial cutting of the stand was found to help oak reproduction by disturbing the site. Fire and scarification were also found helpful if there were adequate light resources available (Arend and Schelz, 1969). The organic layer is also important for species persistence.

The organic layer prevents the desiccation of the seed, if the acorn is below the litter, and the seedlings. Litter depth of 2.54 cm is ideal, with greater depths producing only slightly greater reductions in water loss (Carvell and Tryon, 1961).

Acorns do not provide as much regeneration potential as their shear numbers would suggest. Sixty to ninety percent of the acorn crop can fall to the ground infested with pests (Arend and Scholz, 1969). The germination percentages of the acorns falling off the tree can be less than 1% (Sander, 1979). The predominant method for regenerating oak in an oak stand is by stump and seedling sprouts, not by acorns (Arend and Scholz, 1969). Acorns are a secondary means of regenerating an oak forest.

In examining an acorn crop in one study, one-half of the acorns were lost to animal predation alone, and four-fifths were lost to pests and animals combined. Approximately 7% of the crop was available for regeneration. Regeneration failure by the remaining acorns was due predominantly to seed, or emerged radicle, desiccation. If the moisture contents fall below 50% in white oak acorns or 30% in red oak acorns, viability is affected (Arend and Scholz, 1969).

Acorns can be destroyed by gall forming cynipids (Callirhytis spp.) and the acorn moth (Valentinia glandulella (Riley)) (Watt, 1979; Silvertown, 1980; Sander et al., 1983). But the major insect pests of acorns are the acorn weevil (Curculio spp.) and the acorn moth (Melissopus latiferreanus Wlsm.). The weevil adult deposits eggs in developing acorns, and the larvae consume all or part of the acorn, usually before the nut falls to the ground. Larvae emerge from the acorn when it is on the ground. The Melissopus moth deposits eggs in the same manner as the weevil, with the larvae usually emerging while the acorn is still on the tree, then infesting adjacent nuts. Melissopus pupates over the winter in the leaves of the forest floor, while the Curculio weevil winters deeper in the soil (Marquis et al., 1976). Insect damage to the acorns will continue through the dormant season. In one study, sound seed was placed beneath the litter in the fall and was found to have a survival rate of only one percent after overwintering (Watt, 1979).

The masting habit

The natural selection pressures that produced the masting habit occur where trees experience high levels of predispersal seed mortality in years of low seed production.

The seed preditors of the tree will have a feast or famine cycle slightly out of phase with the seeding cycle of the tree. In the forest, those trees considered to have a masting habit are oak, aspen, basswood, and elm. Those species considered to be non-masting are maple, hickory, ash, cottonwood, and cherry. Masting trees may have an advantage over non-masting trees by having higher seed survival rates. The highest mortality rates usually expected from seed fall are 80% in white oak, 65% in red oak, and 97% in sugar maple. The high mortality rate in sugar maple stems from the poor viability of the seeds (Silvertown, 1980). Table 2 presents the time between large seed crops and the minimum seed bearing age for the three major species of eastern Iowa.

TABLE 2. Time between large seed crops and minimum seed bearing age of selected species (Waller, 1979)

species	years between large seed crops	minimum seed producing age
sugar maple	5 (years)	30 (years)
white oak	7	20
red oak	4	25

Since the oaks are considered masting trees, examination of a tree masting model was completed. If the

mast model calculations are made for red oak using the quantities of 5 years between large seed crops and comparing a slightly increasing (i.e., value of 1.16) population level with a slightly decreasing (i.e., value of 0.84) population level, as could well be the case in eastern Iowa, the model shows little real change in the amount of viable acorns that could be produced. The absolute number of acorns is estimated to be different in the two situations, but the percentage of viable seeds among the mast will be capable of reproducing at roughly equivilent levels (Waller, 1979). Although the ramifications of this theoretical model in the field remains to be seen, what can be discerned by examining the mast model is that for the total population level of oak to fall, as has been suggested in eastern Iowa, either the acorns are being destroyed or made non-viable to a greater degree than in the past, or juvenile mortality is greater now than in the past. The increasing mortality of the acorns or the seedlings over time may be causing regeneration failures.

Acorn dispersal

Short range dispersal of acorns can be by gravity, squirrels, mice, and voles. The animals gather the acorns, then cache them singly or "in mass" in tree cavities, holes

in the soil, or under the litter. Some of the acorns are later removed and used. Rodent caching might play some role in regenerating oaks by specific acorn placement on microsites with good growth and survival qualities (Sander, 1979; Sander et al., 1983). In Missouri, it was found that 99% of all fallen acorns were eaten by vertebrate seed predators, suggesting that even in good acorn production years, seed predation is intense. The pattern of the acorn distribution around a site by rodents followed a negative exponential curve as the distance from the acorn-fall area increased, therefore, few acorns can be expected to be transported by rodents beyond 20 meters from where they fall (Sork, 1984).

The longer range distribution of acorns over a site can be by several specific animal vectors. Red (Tamiasciurus hudsonicus loquax) and fox (Sciurus niger rufiventer) squirrels are travelers and may scatter-horde acorns over an extended area. Gray (Sciurus carolinensis) and flying (Glaucomys volans volans) squirrels are more restrictive to a specific territory in their scatter-hording of acorns (Johnson et al., 1981). White oak acorns are preferred by these squirrels over red oak acorns, and therefore, may be better distributed or consumed quicker than red oak acorns. Oak acorns, though, do not provide a metabolically complete

diet for squirrels and so must be supplemented with other foods (Short, 1976).

Blue jays (Cyanocitta cristata) can act as long-distance dispersal vectors of acorns. Jays have been cited in the United States and Europe as moving large numbers of acorns over 5 kilometers to caching areas along forest edges and in open fields (Johnson et al., 1981). Jays removed as many as 58% of the available mast in a Virginia study. Of the remaining acorns, 43% were eaten by the jays, with the rest destroyed by weevils. Only a small number of viable seeds could be found beneath the tree. The jays began harvesting the acorns from the upper crown, moving to the lower limbs and then to the ground. Acorn cap counts beneath the trees were found to be more accurate at gauging acorn crops, since the caps are usually removed before transporting. Acorn caching sites were found on forest edges and in areas with bare soil. Most acorns were deposited on the soil surface and then covered with litter. The acorns were always cached singly in small caching areas or fields. Germination success of cached acorns was considered to be excellent because of the site selection, with future growth potential considered excellent because of the good light availability (Darley-Hill and Johnson, 1981).

Sprouting

In natural seedbeds, most first-year seedlings of oak come from acorns that are in the soil, or in the humus layer, and covered with litter. Survival of the seedlings is not expected for more than a few years under dense crown and/or understory cover. Under moderately dense canopies, seedlings can survive for several years, but the tops usually die back to the root collar. New sprouts then form from dormant buds and grow. The result of the top dying back repeatably, with subsequent resprouting, is the production of a growing shoot that will be potentially larger than the preceding shoot because of the continually growing and expanding root system. The electron or carbon "investment" by each new shoot in root system size provides the shoot with rapid expansion abilities should additional resources become available (Arend and Schelz, 1969; Watt, 1979; Sander et al., 1983).

Oak regeneration on a site will slowly develop size and interference capability in the understory. If the seedlings-sprouts are large enough and can continue to gather available resources, overstory removal will allow the regeneration to become a part of the new canopy (Sander et al., 1983). Approximately 80% of the regeneration in a stand will be these seedling sprouts. Most oak regeneration

found in the understory then, are not true seedlings but seedling sprouts where the top of the plants have died back with continued resprouting (Arend and Scholz, 1969; Watt, 1979).

After several years of growth, the stem will finally start to interfere enough with other individual stems on the site to move into dominating positions (Watt, 1979). Oak reproduction in the forest is successful, in part, due to the ability to resprout when the top is damaged or destroyed. The resprouting ability is due to dormant buds along the stem, with the highest concentration in the root collar area. The buds sprout when released from domination from more acropetal tissues (Arend and Scholz, 1969).

After harvesting, the types of oak reproduction found in an oak stand are stump sprouts from harvested trees, seedling-sprouts from smaller trees damaged or cut in harvesting, and true seedlings. Older stems may not have been damaged but may sprout spontaneously due to environmental changes in the stand. Sprouts are the more valuable reproduction because they will grow considerably faster than seedlings. Stump sprouts may account for a large proportion of regeneration stocking on a site (Johnson, 1975; Sander et al., 1983).

If the sprout arises from a position below the ground level or low on the stump, and arises from small diameter stumps, the sprout should grow quickly, have good potential for being a crop tree, and have little decay present. Seedlings established after a harvest cut will grow slowly and seldom live more than a few years. Seedlings established before harvest, if damaged or cut, can produce high quality seedling sprouts. Sprouts from both advanced seedlings and from stumps have the potential for properly regenerating a site (Sander et al., 1983).

The procedures for maximizing sprouting are: 1) Cutting should be completed in the dormant season. 2) Cutting should be as low on the bole as possible and should not damage the bark on the stump. 3) Unwanted advanced growth of other species should be removed in a cleaning operation. 4) The oak stump sprout clumps should be thinned before the stand is 20 years old to maximize growth potential. 5) The best formed, most widely-spaced, low-origin, dominant sprouts that have U-shaped vascular connections to the stump should be favored in clump thinning. 6) Maximum space for sprout crown development should be provided. 7) Mature trees should be cut as small groups to allow direct sunlight to enter the opening for the sprouts to utilize (Stroempl, 1983; Arend and Scholz, 1969; Johnson and Rogers, 1980; Tubbs, 1977b).

The sprouting ability expected from a given stump is dependent upon the size of the tree before cutting. The larger the stump, the greater the root potential for powering faster growth, but the greater the chances for pest attacks, desiccation, and poor dormant bud growth that will inhibit sprouting (Johnson, 1979).

Another researcher found that the sprouting ability of oak was not related to the season of harvest, site quality, the vigor of the pre-cut tree, or the DBH of the pre-cut tree, except in red oaks where large trees did not sprout (Wendel, 1975). But, following the general concensus of the literature, studies with black and white oak suggested that the optimal size for sprout production was found to be 15.2 cm in stump diameter, with a general sprout production size range of 10-18 cm in stump diameter. The saplings of this size, if cut, will contribute significantly to the next stand (Johnson, 1979). In white oak, overtopped stumps were found to sprout as often as stumps in the open. Trees over 60 years of age and/or over 20 cm DBH produced few or no sprouts. Age or size of the mother stump had little effect on the height growth of the stump sprouts (McGee, 1978).

Most sprouts leaf-flush 2 or more times during the first 13 weeks of the growing season. Seedlings and mature trees usually flush only once. A reason suggested was that

declining root/shoot ratios result in longer periods of time needed to regain root-shoot balance after shoot growth (Johnson, 1979).

White oaks in West Virginia showed good potential to produce seedling sprouts, while red oak and sugar maple showed poor potential. This suggests that oaks, as a group, do not sprout better than species associated with them (Powell and Tryon, 1979). Generally, the red oak group will sprout more than the white oak group. Also, smaller trees tend to sprout more than larger trees when cut (Sander et al., 1983).

The difference between the age of the shoot and the age of the root stock of a seedling-sprout was estimated in West Virginia. The red oak seedling-sprout root age in years was equal to:

root age = 2.284 + 0.180 * (root diameter 2.5 cm below the root crown) + 0.632 * (stem age in years at 2.5 cm above the root crown)

R-square = 0.882

For white oaks, the root age of seedling sprouts in years was equal to:

root age = 2.741 + 0.169 * (root diameter at 2.5 cm below the root crown) + 0.740 *

(stem age in years at 2.5 cm above the root crown)

R-square = 0.884

Both models are highly significant. The age should be within a plus or minus 4 years (Tryon et al., 1980). If 1 cm is input for the root diameter and 1 year old is the age of the shoot, then in red oak and white oak the age of the roots would be estimated to be 3.06 and 3.65 years, respectively.

Decay has been a concern in stump-sprout regenerated forests. Sprouts arising lowest on the stump were shown to be the least likely to become decayed. Low cutting of the stumps, burning the site at the time of the cut, and subsequent sprout thinning, minimized much of the butt rot present in the stand. The high stump cutting of the past has led to a large amount of butt rotting problems in the current stands (Roth and Hepting, 1969). In seedling sprouts, decay should not be a problem, since no heartwood is usually present when the seedling is cut (Watt, 1979).

Silvicultural systems

Cultural techniques to enhance advanced oak reproduction have yet to be developed (Sander, 1977). The

composition of the next stand will be largely predetermined by the composition of the present understory at the time of cutting. A reservoir of seedlings and sprouts, built up over the years, will insure successful regeneration. The amount of advanced oak regeneration present is a function of the site, not the total amount of seed fall. White oak reproduction is more effective at establishing and persisting in a stand than red oak reproduction. Persistence in a stand is far more important for stand regeneration than initial establishment (Carvell and Tryon, 1961).

Regeneration in oak stands comes from three components. The components are seedlings, seedling sprouts, and stump sprouts. The 10 year survival of these regeneration types was 79% for seedlings and 95% for the sprouts in one study. Seedlings will grow much too slowly to interfere with other species on the site. Sprouting is the dominant form of regenerating an oak stand (McQuilkin, 1975).

Uneven-aged systems Single tree selection does not perpetuate oak stands (Arend and Scholz, 1969; Sander and Clark, 1971; Sander et al., 1983). Selection cutting in a stand yields an understory and reproduction growth increase for only 5 years. Growth stagnation due to resource dominance and preemption occurs (Sander and Clark, 1971).

Single tree selection also holds a more uniformly dense canopy cover with smaller canopy gaps which allow the more shade-tolerant species to regenerate and grow. If more than one tree is selected at a time, more light can be made available (Arend and Scholz, 1969).

Group selection will work to regenerate oak if the cut areas are about 0.4-0.8 ha in size. The regeneration will be poor at the edges of the openings due to severe interference from the edge trees. Regeneration will be good in the middle of the group-selection cut. The group selection system will lead to difficulties in regulating size class distributions and sustained flow of products from the forest (Sander et al., 1983; Sander and Clark, 1971). The use of small group selection will favor white oaks and hickories over red oaks (Schlesinger, 1976).

Even-aged systems For oak to be maintained in a stand, even-aged management will best satisfy reproduction and growth requirements. Advanced regeneration though, must exist on the site for any silvicultural system to successfully function. Seed-tree systems are the least useful even-aged system due to little expected long distance dispersal of acorns and slow seedling growth. Clearcutting regenerates oak, for the most part, on sites that have oak site indexes below 70. Above an oak site index of 70, the

sites will regenerate with greater diversity, and the oak will be of less importance compositionally (Sander et al., 1983).

Clearcutting Clearcutting will work to regenerate oak (Roach and Gingrich, 1968; Johnson and Jacobs, 1981; Arend and Scholz, 1969). Clearcutting a stand should generally lead to regeneration composed of two-fifths shade intolerants, one-fifth shade intermediates, and two-fifths shade tolerants within a forest that contains species having a mix of tolerances. Oak could be considered intolerant to intermediate (Leak et al., 1969). Natural reproduction will develop best only where the overstory has been totally removed and under full sunlight (Sander, 1978). Since all species require an increasing amount of light to maintain rapid growth over time, clearcutting leads to the best growth (Sander and Clark, 1971; Arend and Scholz, 1969).

Shelterwood systems are unable to produce the regeneration stocking required to meet stocking standards. Reducing overstory density by shelterwood might also allow the understory to totally dominate the site for years (Johnson and Jacobs, 1981). Shelterwood was found to not increase the amount of oak regeneration present. The effect of the first shelterwood cut lasts only about 5 years in

increasing growth. Clearcuts will lead to the fastest height growth (Sander and Clark, 1971).

To regenerate oak by clearcutting, harvest cuts or openings should be at least 2 tree heights of the residual stand in diameter, or 0.14 ha at the absolute minimum, to maximize light input and minimize the interference from the residual stand edge. Harvest-cut opening diameters of four tree heights or 0.57 ha would be closer to ideal. If the seedling is to receive two-thirds full sunlight, the diameter of openings should be four times the tree height on level ground, to sixteen times the tree height on north slopes (Fischer, 1979). Therefore, the minimum size of a circular clearcut is 0.20 ha, with 0.41 ha being ideal. If the clearcut is not circular, then 0.41 ha should be the minimum cut (Sander and Clark, 1971; Arend and Scholz, 1969; Fischer, 1979). Usually, the suggested size of a clearcut is 0.81 ha or larger (Sander et al., 1983).

In clearcuts, it was found to be more practical to prevent unwanted competition soon after harvest by herbicide, rather than by later thinnings (Johnson, 1976a). Weed species in the understory do not prevent the regeneration of a crop species but greatly slow the growth of the crop species. Cutting or killing unmerchantable species or individuals after clearcutting is required. Oaks

present on the site, especially if of poor form, should also be cut at the ground level for resprouting. Advanced reproduction may not be needed if harvesting cuts coincide with good acorn crops and interference is controlled (Johnson and Jacobs, 1981; Sander et al., 1983).

Herbicide applications after clearcutting were found to be more successful at controlling interfering vegetation than application after the harvest cut of a shelterwood, because of the destruction of the advanced reproduction in the shelterwood along with the other vegetation. Where the shrub layer was found to be limiting the regeneration of oak, the removal of a portion of the canopy, as in shelterwood, increased the importance of the shrub layer (Johnson, 1976a; Johnson and Jacobs, 1981).

Advanced reproduction is the major form of the regeneration. Rarely will new seedlings reach dominance in a clearcut. Since oak regeneration depends on advanced reproduction, there is no need to wait for good seed years (Roach and Gingrich, 1968). The amount of oak present in a stand is set at harvest time (Sander, 1978; Sander and Clark, 1971). Clearcutting can be used to regenerate oak if advanced reproduction is present (Sander, 1978; Sander and Clark, 1971). Cutting should also try to coincide with bumper acorn crops (Johnson and Jacobs, 1981). Shelterwood

must be used if advanced reproduction is not present. Advanced reproduction must be large and have large root system size. Seedling sprouts are the preferred regeneration type. New oak seedlings established at the time of harvest are of no significance in reproducing an oak stand (Sander, 1970).

New seedlings in clearcuts grew slowly and became suppressed after 6 years. Oak seedlings coming into the stand after harvest will never reach the new canopy level. The size of the clearcut did not effect the regeneration present but did effect its growth due to the border effect. For regeneration, the edges of the smallest opening are least favorable and the center of the largest opening is the most favorable, assuming tree reproductive systems are available on the site (Minckler et al., 1973). All openings have a border approximately 6.1 m wide where reproduction is inhibited due to resource dominance by the surrounding forest trees. Small openings have a greater percentage of their area occupied by this anti-reproduction zone than larger openings. Clearcutting can help magnify this attribute of forest openings (Sander and Clark, 1971; Minkler et al., 1973).

Clearcutting will be successful in regenerating oak if the advanced reproduction meet certain minimum levels of

stocking. Trees that are 5 cm in diameter, at breast height, should amount to 3089 trees per hectare, based on a tree horizontal crown area of 0.0003 ha and 2 m spacing (Roach and Gingrich, 1968). When the advanced regeneration is at least 1.37 m tall, including stump sprouting potential, there should be at least 1075 well-distributed stems per hectare to regenerate an oak stand (Sander, 1978; Sander et al., 1983). Advanced reproduction of 546 well distributed trees per hectare in the 3 inch size class is considered a good stocking level (Johnson and Jacobs, 1981).

Therefore, the proper amount of advanced reproduction on a site will be at least 1075 oak stems per hectare over 1.37 m in height. If less than the proper stocking amount is present, the stand should not be harvested until this reproductive stocking level is reached. Stump sprouts may make up a portion of this reproduction stocking (Sander, 1978). Stump sprouts alone should not be relied upon for regeneration of a site (Sander et al., 1983). When adequate advanced reproduction exists on a site, the use of a shelterwood system will have no major regenerative advantage. Shelterwood should be used only where advanced reproduction is not present or where the advanced reproduction is too small to reach regeneration stocking minimum requirements (Sander, 1978).

Epicormic branching has been considered a distinct problem with residual trees after a regeneration treatment, especially after clearcutting. Openings 45.7 m in diameter had as heavy epicormic branching as larger diameter openings while openings less than 45.7 m in diameter showed much less epicormic branching. Dominant and codominant trees did not produce as many epicormic branches as lower crown classes. Epicormic branches do increase with height up the bole. Many epicormic branches are small and short-lived on the oak, having a minimum of degrading effect on the value of the wood. The initiation of epicormic branches is directly proportional to the number of live branches present on an edge tree. Stand density and relative vigor of the edge tree are important in the persistence of epicormic branches. To minimize defects, oaks should be cut in clearcuts as large as possible to minimize the edge effect on increased epicormic branching (Trimble and Seegrist, 1973; Ward, 1966).

Clearcutting, however, is not the perfect system for regenerating oak. A clear example of the oak regeneration problem is encapsulated by a study in Pennsylvania. Clearcutting a stand with 90% of the basal area in oak yielded a stand with only a minor portion being oak after 15 years. Fast intolerant trees occupied the site, formed a

canopy, and suppressed oak stump sprouts. Only 3% of the stump sprouts and none of the seedling or seedling-sprouts had assumed dominance on the site (Ward and Bowersox, 1979).

Shelterwood Other workers have found that shelterwood seems to be the desirable silvicultural system to regenerate oak (Merritt, 1979; Schulz, 1952). Shelterwood helps to maintain superior growth rates and efficient nutrient cycling in a stand (Stone et al., 1982). Shelterwood, as applied in the past though, has not resulted in establishment of substantial new oak growth and has failed to provide for continual oak survival and growth. The classical shelterwood system does not regenerate oak well. Therefore, there is a need to develop a shelterwood system that will. Key points in any oak shelterwood system have been to leave a greater density in the original stand after the regeneration cut, to have more patience waiting for oak regeneration, and to spend more time nurturing the regeneration developed (Sander, 1977).

Shelterwood systems should be used where there is little advanced regeneration present. A series of shelterwood cuts should maximize the establishment of new oak seedlings and/or provide for the development of any small existing regeneration. The regeneration cut should leave a uniform density canopy by thinning from below and

being sure to leave no large canopy holes. The understory will need to be controlled, and individual stem treatments are suggested. The time period until final harvest should be 15-25 years after the first cut. As the stocking reaches 75%, the stand should be cut back to the 60% stocking level. If the oak regeneration is over 3 feet tall, cutting back to 50% stocking will help the growth of the regeneration. When the stand has 1075 advanced regeneration stems or more, that are over 1.37 m tall, per hectare, the final cut can then be made (Sander, 1978 and 1979). The first cut should be timed to coincide with a good acorn production year. Thinnings in the stand at 50-60 years into the rotation could be the beginning of a shelterwood regeneration system (Sander et al., 1983). After light cuts, the light limitation is usually from the canopy, while after heavy cuts the limitation is usually from the understory (Sander, 1979).

Shelterwood offers a good way of getting advanced reproduction started over a 20 year period. The germination and survival of acorns were found to be better at stand densities of 50-70%. After 3 years, 50% of the seedlings established survived. Small oaks did not need additional help in interfering with surrounding vegetation (Sander, 1979). The final removal cut of a shelterwood should be timed to occur when sprouting will be maximized (Sander, 1978).

Advanced and planted oak reproduction must be allowed to reach 1.37 m tall before the harvest cut, or the site will not regenerate oak. The time required to produce strong advanced regeneration is approximately 10 to 20 years. The overstory during this period should ideally be maintained at a 60% stocking level. The occurrence of oak in the new stand will be proportional to the amount of oak in the advanced reproduction. Advanced reproduction is often unrelated to species occurrence in the overstory (Sander, 1977).

A slightly different regeneration approach is suggested by Perkey (1984). The first shelterwood cut should be made at times of bumper seed crops or for two years thereafter. The trees, after age 55, are large enough and old enough to produce enough acorns for all the pests on the site, with some acorns available for regeneration. Trees remaining after the first cut should be dominants with great potentials for heavy acorn yields. The first cut should remove 50% of the crown cover. Once 70% of sampled mil-acres are stocked with two foot tall oaks, the overstory may be removed.

Another shelterwood approach is offered by Arend and Schulz (1969). Shelterwood systems can work well if the first cutting removes 30-50% of the basal area. On sites

having nc shrut compcneat, crown ccver could be thinned to 50%. If the sites have a good shrut compcneat, then the crown cover should be thinned to only 75% of total coverage. Crown thinning should favor dominants that are good seed producers. In shelterwood, older, larger trees of poor form should be harvested at least 10 years before final harvest to provide additional resources for reproduction.

New seedling establishment in a shelterwood depends upon a good accrn crop, so at least 5-10 years should be allotted tc wait for proper regeneration to get started. Seedbed preparation can help establishment if it ccincides with a good seed year. The sites usually must be continually treated to remove weed species. The light intensity under which oak reaches near maximum photosynthesis is 30% of full sunlight. To have this light intensity at ground level requires a crown thinned to 80% of overstory stocking with no understory. This means that strict understory control is needed (Sander, 1979).

In regenerating an oak stand, the amount of reproduction of a given species was found to be poorly related to the amount of that species in the canopy. The lack of light seemed to account for the absence of oak regeneration. Partial cutting allowed more oak to regenerate than clearcutting. Stump sprout reproduction was

not affected by cutting method and, after 2 years, made up only a small proportion of the stand. Of the oak stems present after 2 years from cutting, 90% were seedling sprouts. The shoots were continually killed, but the roots continued to survive and grow. Seedling sprouts are the preferred type of oak regeneration. Seedlings grow slowly and seldom gain dominance. If a stem does not become established in the first year after clearcutting, the stem will seldom grow into the dominant canopy. Oaks should dominate the site by 12-15 years after cutting, if they will dominate the site at all (Sander and Clark, 1971).

Specific silvicultural recommendations for eastern Iowa

The recommended harvesting system for eastern Iowa, in general, is clearcutting (Sander, 1977). Regenerating oak in the driftless area of northeast Iowa does present many problems. Clearcutting reduces the relative importance of the oak in a stand by allowing more cherry and hickory colonization. Sugar maple and basswood take over sites only when they have high importance values in the stands and usually only on good sites. In this area, many early to intermediate successional stage forests are dominated by red oak with little advanced reproduction. After clearcutting, seedlings and seedling sprout regeneration reach maximum

importance in red oak stands after 12 years and in white oak stands after 16 years. Regeneration failure of oak is thought not to be due to the lack of establishment, but to inadequate growth rates. Low light levels and low soil moisture inhibit root growth, and therefore, few seedling root systems are capable of supporting the rapid growth needed to enter the canopy. Most clearcuts average 173-247 good oak stems per hectare at age of 25 years. This stocking level is only one-third of suggested minimum stocking for oak (Johnson, 1976b).

Sander (1977) recommends, in mature stands of northeast Iowa with oak site indexes of greater than 75, that the stand should be converted to other hardwoods. If the stand would have at least 66% of its basal area composed of oak, then manage for oak through the current rotation. Ecological trends clearly indicate that replacement of oak on good sites will occur by more mesic species. Red oak and red oak-white oak mixtures are ecologically unstable in northeast Iowa. It is not usually practical to manage for oak in this area. Harvesting in northeast Iowa results in mixed oak stands, with weeding required as early as age 5 with careful attention required for the oak reproduction. Future stands will contain only sprout-origin oaks with eventual domination of the sites by more mesic species. The

species that should be managerially preferred are white ash, sugar maple, basswood, black walnut, and the oaks, if possible. Table 3 provides expected rotation periods and diameters for given sites (Sander, 1977).

TABLE 3. Expected rotation lengths and diameters on three different site quality types for oak (Sander, 1977)

oak site index	site quality	rotation length	expected diameter
>75	good	60-70 years	24-28 DBH
55-74	average	75-90	20-24
40-54	poor	90-120	16-19

Site preparation for natural and artificial regeneration by soil scarification has not been shown to be beneficial. Planting has not been tried or proven satisfactorily. Planting, if attempted, should be at the 500-600 stems/acre level with the largest planting stock available. The larger seedlings survive and grow better in the stands because of their large root system size. The root system size is critical to the success of the seedlings over time. Planting after clearcutting has not worked in the past due to slow seedling growth (Sander, 1977).

Thinning

The basal area of the stand can affect the regeneration present and its growth. In stands with low basal areas, large trees grow at near full potential, while regeneration grows at a reduced rate. In stands with high basal areas, large overstory trees grow only a small amount, and growth of the understory is restricted (Holdaway, 1984). Lower basal areas usually mean a greater availability of resources on the site. Thinned stands are more resistant to drought than unthinned stands and can often better withstand attacks of secondary agents of injury. Removal of low vigor, defective trees by thinning minimizes wood boring insects in the the stand (Sander, 1977).

Thinning stands help build up the advanced regeneration on a site (Arend and Scholz, 1969). Oak seedlings persist and build-up over time in the understory of the more open stands. In more closed stands, thinning is required to insure oak survival and growth. In the understory, the crowns of the oak reproduction should have a distinct leader, or a more excurrent branching form. Flat-topped seedlings should be cut at the base for resprouting otherwise these seedlings will not respond quickly to release. Drier sites usually have adequate light on the ground surface to allow waves of oak regeneration to survive

and grow. Thinning to increase light quantity is required on moister sites (Carvell, 1979).

Oak reproduction is determined by seed-fall patterns often characterized by dense clumps and open spaces. In early growth (i.e., 0-20 years), light and physical space are more important to the trees than soil nutrients and root development space. Height growth is rapid, and trees that are over-topped will quickly die. If dominance of the site is not reached or maintained by a stem, death will occur within a few years. Once a stem has experienced a period of slowed growth, reponse to release may be poor. The stocking level at the 20 year mark should be approximately 300 crop trees per acre with their crowns released. Everything else on the site should be left in place (Gingrich, 1979).

After any harvest cut, weeding will probably be required for at least 10 years to eliminate interference and to thin stump sprouts to one or two per stump. Thinning should start between ten and twenty years and then every 10 years. The total growth and wood production in oak stands will remain essentially the same over a wide range of stocking levels as long as there are enough trees to utilize the site. The rotation period can be shortened by thinning and maintaining low stocking levels, due to fast individual stem growth. Large canopy gaps should not be allowed to

occur, since this will favor the shrub component. One large thinning is not as good as several smaller thinnings, because the trees will be functioning at non-optimum conditions for longer periods of time if thinned only once. The remaining trees also have a greater chance of developing epicormic branching. Thinnings should end after approximately 75% of the rotation is over. Thirty years prior to harvest, advanced regeneration should be encouraged to establish and grow (Sander, 1977; Sander et al., 1983).

When thinning stands that have not been previously thinned and older than 30 years, thinning should be back to the 70% level for the first time. The tree crowns will not be able to expand rapidly enough to fill in the spaces of a greater thinning, and epicormic branching may lower the quality of the stems. Gradual thinning of the canopy from below is needed to slowly bring the stand to proper stocking. The subsequent thinnings should be back to the 60% stocking level (Sander, 1977).

Another thinning approach is for the first thinning to be completed when the trees are from 4.9-6.1 m tall. Species interfering with the oak regeneration should be removed. Fifty to seventy years into the rotation, thinning should be stopped. Live crown ratios of 30-50% should ideally be maintained on oaks (Arend and Scholz, 1969).

Thinnings favor the most dominant trees on the site by increasing diameter growth. In one study, the site was found to not greatly influence growth rates of oaks after thinning. Thinning was found to significantly lower rotation age by continuing rapid growth of the stems (Hilt, 1979). The form class of upland oaks were not changed significantly by changes in stocking levels (Hilt and Dale, 1979).

Stand structure has little effect on volume growth and on the stocking level present, within reason. Understocking in young stands is not serious, provided the trees are well-spaced. In stands that are 100% stocked, 40% of the basal area can be removed without a loss of volume growth (Gingrich, 1967).

Crop-tree release studies in West Virginia on red oak and sugar maple showed that, five years after releasing, only 23% of the trees were still potential crop trees. The trees were nine-year-old, seedling origin, crop trees that were 4.9 m tall, in a clearcut area. Release did not prevent crown-class regression. Release did not improve height growth, diameter growth, or length of clear bole present. Releasing crop trees is considered inadvisable at the 9 year-old stage for red oak and sugar maple. Crop trees should not be released until they reach 7.6 m or more in height (Lamson and Smith, 1978).

If the number of crop trees per acre is known, the spacing between them can be determined by taking the square root of the product of 43,560 divided by the number of crop trees. The spacing is in feet and can act as a guide for proper thinning of stands (Leak et al., 1969).

The effects of a thinned canopy on the understory is not known. In oak stands with stable canopies, the understory of shrubs and herbs were found to radically change over time. The understory was found to change in composition in an uncorrelated manner with the canopy (Davison and Forman, 1982).

Artificial regeneration

Planting or interplanting can work with acceptable survival, but long establishment periods and slow growth can cause extended rotations, in the least, and eventual death of the seedlings at most. Interfering vegetation control is required for a few years after planting. Direct seeding can work if repellents are used to prevent pilferage by rodents. To date, there has been no fully successful repellent developed, and mechanical protection is too expensive on a seedling survival basis (Sander et al., 1983).

Underplanting can be successfully used to increase crop species establishment (Sander, 1979). Both direct seeding

and planting can regenerate oak. Overtopping herbaceous vegetation and woody shrubs must be eliminated for good survival. Animal damage seems to be cyclic and occurs predominately in the winter. Some type of anti-predation system is needed for acorns and seedlings for success (Scholz, 1964).

Direct seeding works better in red oaks than white oaks because of problems associated with white oak acorn collection and storage. Rodent control is required to have any chance of seed germination and growth (Arend and Scholz, 1969).

The best way to maximize the germination of white oak was found to be sowing them in the fall immediately after collection. If storage was required, then the acorns should be stored at 2-3 degrees Celsius in 1.75 mil polyethylene bags, or cloth bags, that will allow for good diffusive aeration. Carbon dioxide was found to build up to high level inside 4 mil thick polyethylene bags and effectively smother the acorns (Rink and Williams, 1984).

The major problem with artificial regeneration, to date, is that seedlings are planted that are too young or not vigorous enough to survive on a forested site with strong interference (Merritt, 1979). In the temperate hardwood forest, 90% or more of the tree feeder roots are

found in the top 7.6-10.2 cm of the soil, rarely going into or below the E soil horizon (Tubbs, 1977b). Interference with the root system of a newly established seedling is great. Failure of plantings for regenerating oak stands is primarily due to the slow growth of the seedlings, not mortality. Spring planting dates are preferred for oak to minimize frost heaving and shoot dieback. Field performance could be enhanced by planting large nursery stock of high physiological quality. The concept of high physiological quality includes having a high level of carbohydrate reserve, having had adequate moisture all growing season, and having been root pruned. The size of the stock should be at least 8 mm at 2 cm above the root collar (Johnson, 1981).

Underplanting to regenerate an oak forest is possible with care. When underplanting, shoot pruning of the nursery stock can increase survival rates. Understory control by herbicides is also needed to insure success. The planted trees must initiate rapid shoot growth immediately after planting, to be successful, and shoot pruning may stimulate this growth. Transplants (1-1) are superior to seedlings (1-0), due to the greater initial root growth rates of the transplants. Underplanting before clearcutting will be much more successful than planting after clearcutting, especially

if adequate time is allowed for seedling establishment. Short pruned (1-1) nursery stock, at least 10 mm in basal diameter, is recommended. Planting beneath stands that have 60% stocking levels, with the overstory to be removed in 3 years, maximizes regeneration probabilities. Planting should consist of at least 2 trees planted for each successful tree required. Preplanting herbicide treatments may also be needed to eliminate interfering species (Johnson, 1983). A note should be made here that a root grading system may greatly improve expectations of seedling survival, and therefore, is needed for oak planting stock.

Interplanted stems have an establishment period, before strong growth occurs, of about 4 years. The knowledge of whether interplanting has been successful may be delayed because stocking guides are usually not practical until the stands are 15-20 years old, so the number of stems needed for a given stocking level is not known accurately. Survival and height growth criteria can show if the planting was successful. The size of the regeneration, rather than the age, should be used for judging the quality of the planting stock. Comparing the relative growth rate of the planted stem with stump sprout growth provides an idea of how well the stem will compete on the site (Johnson, 1976b).

Artificial regeneration of oaks by planting can be unsure, due to the slow initial growth of red oak seedlings. The slowness of early growth can be partially overcome by planting large, vigorous nursery stock. Picking the red oaks in the nursery bed with the greenest foliage through mid-fall, then with a rapid loss of leaves, will insure the best seedlings to plant (Larson, 1977).

The new shoot growth of oak seedlings is correlated with the root weight of the seedling and/or the root/shoot ratio. Shoot-pruned trees were found to break bud two weeks earlier than unpruned seedlings. Shoot pruning in spring after lifting has little adverse affect on root growth (Larson, 1975). The longer the leaves are kept on the seedling in the nursery, or in the field, until a killing freeze, the better the growth expected the next growing season (Larson, 1978).

Survival of understory oak is a question of differential species tolerance and growth. Tolerance is the adaptability of a species to competition for light, water, and nutrients. Intensive cutting of the overstory and the understory was required to insure survival and growth of underplanted oaks. Herbicides were effectively used on the woody understory (Gatherum et al., 1963).

Cultural treatments of seedlings, such as the addition of nitrogen, phosphorus, mulches, and pruning treatments, did not affect seedling growth when outplanted. large seedlings kept their height and growth advantage over the smaller seedlings. Both 1-0 and 2-0 seedlings could reach at least 1.8 m tall in seven years, so they would be able to interfere well with other species. The 2-0 stock was best to plant, but the 3-0 stock in this study had roots too large for conventional lifting equipment, and therefore, were not properly included in the study. Using an auger to dig the planting holes was the preferred system for planting. In this study in West Virginia, 30-50% of all trees planted were expected to reach maturity (Wendel, 1980). Artificially regenerating a site in West Virginia with containerized stock was unsuccessful because of rodent damage to the trees. Seedlings (1-0) from a nursery worked the best on regenerating a cut-over site (Wendel, 1979).

The primary cause of oak regeneration failure in Pennsylvania was suggested as an absence of viable acorns. Pests, predominately insects and rodents, destroyed most of the acorns even in good seed years. Direct seeding of oak has a potential problem because of predation from rodents, since insects are more closely tied to the flower-fruiting cycle. Protection with plastic guards was ineffective.

Effective repellents are needed in order to use direct seeding. Planting stock has been damaged by deer browse but it is the most promising artificial regeneration technique. Protection devices may be required. Different stands differ in the amount of seed-pest problems encountered, even when near each other. Since the lack of viable acorns is the primary cause of regeneration failure, shelterwood will not produce a stimulation of regeneration unless insects and/or rodents are controlled (Marquis et al., 1976).

Improving the survival and growth of outplanted oak seedlings is possible with proper application of mycorrhizal technology (Garrett et al., 1979). Improvements in planting and seeding may also come from the field of tree genetics. Genetically, oaks in the central states have been victims of dysgenic selection processes, or high-grading. The best genetic sets have been removed with the poorest gene sets left to reproduce. Oak has great genetic variability, and therefore, a great potential for good trait development through breeding. Planting of superior genetic stock could greatly improve establishment and growth of oak on forested sites (Beineke, 1979).

Regeneration stocking measures

One measure of the adequacy of regeneration on a site is to sample the area to determine the number of 1/1816 ha plots that contain oak stems 1.37 m tall and less than 5.1 cm in DBH. The percentage of the sample plots stocked with at least one stem meeting the criteria put forward is the regeneration stocking level, assuming enough plots were taken for the sample area. If regeneration stocking levels are greater than 59%, there is adequate advanced reproduction present to regenerate the site. If the regeneration stocking is less than 59%, stump sprouts may be able to make up the difference in regeneration stocking. If the regeneration stocking, including the stump sprouts, still falls short of the 59% value, then do not harvest the stand until regeneration stocking levels reach the 59% level (Sander, 1977; Sander et al., 1976).

In order to harvest-cut a stand, the stump sprouts in a shelterwood after the regeneration cut should ideally be at least 1.3 cm in DBH to insure good interference. This size of stump sprout must be coupled with advanced reproduction of the proper size, in order for the site to regenerate oak (Sander, 1971).

Another regeneration stocking level recommended was 989 trees/hectare of advanced reproduction, 0.31 m or more in

height. If adequate advanced reproduction was present, the overstory could be completely removed. Partial cuttings could be used to stimulate advanced reproduction if there was not enough. As a general rule, the better the site, the less oak regeneration expected. Dominance of the site after cutting was by the species whose advanced reproduction was the tallest at the time of cutting. Past disturbance was positively correlated to the presence of advanced reproduction, and direct sunlight was required to maintain the interference capatilities of the regeneration (Arend and Schelz, 1969).

The newest and most interesting regeneration stocking guide for the Missouri Ozark area suggests that the average stocking value for adequate advanced oak regeneration is 30% (221 stems per acre). The average stocking value is calculated from individual plot stocking values that are, in turn, determined from the aspect, slope position, height, and ground diameter of the tallest oak stem on the regeneration plot less than or equal to 3.8 cm DBH. A potential stump sprouting level can also be determined from the DBH class, site index, age, and species of the overstory stems to supplement any advanced regeneration shortages. The stocking value reference calculations were derived from the contribution of a single stem to the stand stocking

value at age 20. See the publication for specific regeneration stocking factors (Sander et al., 1984).

It has been suggested that far fewer seedlings of red oak per acre are needed to constitute adequate stocking. Only 112 well-distributed and well-established seedlings or sprouts per hectare are sufficient to allow red oak to dominate a site. The other trees on the site help to "train" the oak and are removed, over time, to provide space and resources for oak developement (Oliver, 1978).

Site Preparation

Soil scarification increases, in the short run, the regeneration of all species on a forested site. Specifically, the disruption of the litter layer assisted oak regeneration (Scholz, 1955a). Regenerating oak on scarified sites over the long run, showed no significant difference with unscarified controls. Scarification improved intial establishment of red oak and other associated tree species, but after 8 years the value of the treatment was greatly reduced. Eliminating grazing from the site also benefited regeneration (Scholz, 1959). Note that in this study, following great initial establishment on the scarified sites relative to the controls, no further treatments were made to insure survival.

litter was found to have an adverse effect on oak regeneration, but scarifying the soil surface after the harvest cut did not increase oak importance on the site. The use of a soil disk after shelterwood cutting increased the establishment of oak, but after two years the advantage in established seedlings was lost. Effective cultural treatments for regenerating oak remain to be developed (Sander and Clark, 1971).

Chemical weed control was found to increase the survival and growth of red oak plantings. Fall plowing and spring disking and harrowing assisted the herbicide effect by allowing herbicides to be applied to bare soil. Site preparation did not increase red oak growth rates more than untreated, herbicided sites (Erdmann, 1967). Preharvest weed species control will usually be required in any silvicultural system (Sander and Clark, 1971).

Fire

The role of fire in oak stands is ancient in extent. Fire has had an important role in the development and maintenance of existing oak-hickory stands. Frequent fires followed the original harvest cuts and tended to eliminate the fire-intolerant species. Oaks sprouted after fires, if the root collar had survived, and occupied burnt-over sites.

Single fires were found not to affect the species composition on the site because fire-intolerants reentered the stand quickly. Multiple fires helped to develop oak forests and eliminated fire-intolerant species by maintaining a continual fire-stressed site condition (Sander et al., 1983). Burning the site after cutting was considered to stimulate oak regeneration, but fire also resulted in a greater shrub component (Arend and Scholz, 1969). The better the site, the shorter the period between fires required to control interfering species (Merritt, 1975).

The effect of prescribed fire in oak stands is not known (Sander, 1979). When the original oak stands were cut, they underwent a series of fires. The recurrent fires were responsible for the current stands. Fire as a regeneration tool in oak stands has not been successful, and therefore, has not been recommended. Oaks are susceptible to fire at all life-stages due to cambial death near the ground. Fire should be completely excluded from oak stands (Sander, 1977). Prescribed fire was found to be detrimental to oak regeneration because the fire killed the shoots and therefore, lost the height growth accumulated (Teuke and Van Lear, 1982).

One fire over a site was found to not change the species composition (McGee, 1979). Prescribed burning with a single spring fire killed many young oak seedlings and failed to control competing vegetation. If the temperature at the root collar went above 140 degrees Fahrenheit, then many seedlings were killed. Short duration temperatures of up to 220 degrees Fahrenheit were survived by 30% of the seedlings. Many of the seedlings sampled that sustained shoot dieback, sprouted back. A single, low intensity, spring fire may do more harm than good to red oak seedlings one year old. Larger reproduction may have a higher survival rate (Johnson, 1974).

The burning of an oak-hickory forest produced two valuable observations. The first is that burning in spring killed all woody stems less than 5 centimeters in DBH. The second was that nutrient loss and depletion caused by periodic burning does not appear to cause long term problems. The vegetation of the oak-hickory type appears to be adapted to annual spring burns (Knighton, 1977).

In Minnesota, red oak was shown to be a vigorous root collar sprouter after prescribed fire. Sugar maple was poor at sprouting. Burning the site did not hinder or aid sprouting as such as encouraging sprouts to originate low to the ground (Perala, 1974).

A twenty-three year old stand of oak in Missouri was burned, then examined. The stand was reestablished by basal sprouts. After 10 years, the number of sprouts per stump ratio had fallen from 5.3 to 1.6. Before the fire, 79% of the trees were oak or hickory. After the fire, survivors were nearly all oak. The results of the fire were a composition shift toward oak and a loss of 23 years of growth (Loomis, 1977).

Selected physiological features

The seasonal stem growth of hardwoods, in general, is proportional to their seasonal leaf area in the shade or sun. Leaf area is increased in the shade, but a genetic ceiling exists for leaf volume and electron/carbon capture. Oak and sugar maple have similar leaf responses to light and similar stem growth responses to shade. There is no correlation between shade tolerance and growth (McClendon and McMillen, 1982). With a canopy opening, regardless of the photosynthetic efficiency in shade, there were no differences in the net assimilation rates between red oak, white oak, and sugar maple (Geis et al., 1971). Oaks do have a greater water-use-efficiency (WUE) than sugar maple. WUE is the transpiration rate over the photosynthetic rate, or the number of carbons fixed for each water molecule transpired (Wuenscher and Kozlowski, 1971).

In Missouri, the shoot and root growth of oaks were examined. In seedlings and trees, root growth was reduced during shoot growth. Only while shoot growth was in a resting phase did roots grow. Both in the understory and in mature trees, there was usually only one flush of growth per growing season. Stump sprouts had multiple flushes of growth. The periodicity of growth, which includes one shoot-growth flush and one root-growth flush, was 38 days. In mature trees, root growth began in spring with increasing soil temperatures. Sometimes the roots were growing for 38 days before the crown. Seedlings did not begin root growth until leaf expansion had begun. In mature trees, the root growth continues into the winter until the soil temperature reached 2.5 degrees Celsius. The result of winter root growth is that the tree continued growth for 64% of the winter period (Reich et al., 1980).

In the oak, most growth processes are either completed or well under way before positive rates of net photosynthesis are achieved (Dougherty et al., 1979). Oaks reach near maximum photosynthesis at one-third of full sun, but the maximum point of height growth occurs in full sun (Merritt, 1979). As the growing season progresses, more and more excess photosynthate is produced in the leaves of oaks. The excess photosynthate is concentrated in the high crown

with less in the lower crown. The carbchydrate reserves of the branch material, used to power spring growth and development, are then replenished. The canopy sinks for carbohydrates are, in order of decreasing importance or strength, acorns and buds, leaves, and trenches (Mclaughlin and McConathy, 1979). In a study of a white oak forest, the roots acted as major carbohydrate sinks in the spring and fall. The crown showed rapid mobilization of carbchydrates and recovery of storage materials from local cell walls. Energy materials were stored in the canopy area for canopy growth the next season (Mclaughlin et al., 1980).

Oak seedlings were found to need relatively high light levels specifically during the July to September period, therefore, interfering species should be removed. A shoot-root ratio of 0.40 or below should be maintained for proper survival and growth. Grass or herbaceous competition eliminated both germination and survival of oak (Scholz, 1955b).

Red oak seedlings growing in shade, and seedlings removed from shaded conditions in January, broke dormancy ahead of seedlings growing in the open or put into the shade in January. The early budbreak increased the chances of frost damage to the leaf material. Budbreak timing was found to be related to the crown conditions of the past

growing season. Harvest during the dormant season can cause regeneration damage due to frost (McGee, 1975).

The allelopathic component of interference in herbacious plants occurring in the forest understory is great. The trees also have an allelopathic component of interference that varies by site and individual (Rietveld, 1979). Red oak and white oak have allelopathic attributes which modify the understory beneath (Lodhi, 1976). The forest is a mosaic of overlapping patterns of leachates, exudates, decay products, and soil influences resulting from the different species and individuals present. The allelopathic component of site interference may be minimized by the use of fire (Rietveld, 1979).

Major Pests

The major pests of oak have the most effect on acorns but mature trees also have problems. Oak wilt (Ceratocystis fagacearum (Bretz)Hunt) usually kills scattered individuals or small patches of oak, as does the two-lined chestnut borers (Agrilus bilineatus (Web.)). Other stem borers and decay organisms can destroy wood value but seldom attack rapidly growing, vigorous trees. The predominant method for controlling pests within a stand is by maintaining a healthy, vigorous stand (Sander et al., 1983).

REGENERATION MODEL CONCEPTUALIZATION

The understanding of regeneration and differential growth is synonymous with the understanding of succession in a forest community. The idea of succession, whether it "exists" in nature or is merely a residual of observation resulting from changes of species along a vegetational continuum, is not of concern. Regeneration exists and its dynamics control the forest in a long-term sense while the trees present on the site control short-term changes. Succession may or may not be an emergent property of a system, nor be necessarily convergent. Succession suggests that species composition is changing over time and regeneration is the vehicle of this change. The following conceptual model (Figure 2) was developed from the literature for regeneration of forest stands. By understanding the dynamics of regeneration, assumptions can be made regarding succession, and these assumptions can, in turn, provide a clearer picture of reproduction in the forest.

The successional literature provides an interesting comparison of philosophies, and a framework that both constrains and allows for the expansion of successional concepts. The literature also demonstrates differing interpretations of oak regenerating forests by researchers.

Tree Regeneration is a function of

Tree Presence
- root and stump sprouting
- layering
- growth rate and form
- sexual reproduction
- canopy position

Seed Dispersal
- methods of dispersal
- dispersal distance
- seed viability
- seed physical characteristics

Site factors
- catchement and lodging
- germination
- growth rate and form of sprouts or seedlings

Social factors
- suppression tolerance
- competition
- allelochemics

Climatic factors
- fruiting and flowering success
- bud survival
- seed survival
- photosynthetic array survival and maintenance

(inherent in all of these components are pest interactions)

FIGURE 2. Components of a conceptual regeneration model for a forested stand

Based on observations from this study, some interpretations seem to be inherently incorrect and require further thought. The following paragraphs coupled with the discussion section will develop a conceptual model of regeneration (Figure 2) and a framework of ideas on the forest community necessary as counterpoint and supplementation to the literature.

Regeneration on a site will be, in part, a function of the trees present on the site, their primary method of reproduction (sexual or vegetative), and their growth rate and form (Figure 2). Occupancy of the site preempts resources from use and can prevent or dramatically change the regenerative status of a site. Regeneration is also a function of seed dispersal. As shown by Horn (1981a), regeneration distribution dictates replacement. In other words, tree regeneration must exist, or propagules must be able to be delivered to the site and establish themselves in order to replace the present occupant. No matter how perfect the site is for a species, if its propagules cannot be delivered, it is meaningless to consider that species as a viable alternative in species replacement. This point of non-statistical dispersal has been overlooked or discounted in some regeneration models. Dispersal of the seed depends upon the method or methods of transport, the distance over which transport can take place, the viability of the seed

versus time and dispersal medium, and the size of the seed (i.e., mass per unit surface area).

Of all the components of a regeneration model (Figure 2), site factors most easily come to mind as limiting regeneration. Site factors include the catchment and lodging factors of a particular area, the seed germination constraints, and the inherent growth rate and form of the seedling or sprout versus resource availability. Site factors can be some of the most readily measurable characters present in an area but may be meaningless or of low correlation with regeneration success. In management, some site factors can be manipulated to increase or decrease regeneration of specific species.

Regeneration can also be a function of the social interaction component of a species and the site. Tolerance of suppression, competition, and allelochemic interactions throughout a lifespan can dictate survival or death for a species. Interspecific and intraspecific interference suppress the maximum potential growth of a tree on a site. If some minimum level of carbon gain is not reached every year, or in some cases, over several years, death will result.

The last component of the regeneration model is the climate, both macro- and micro-climate. The climate

determines potential limits of the geographical range of a species, determines flowering and fruiting success, and determines the survival of the vegetative buds, supporting tissues, and seeds. Subtle changes in microclimate have been shown to radically change species survival. Microclimate characteristics, especially at the seed-seedling level, can entirely change the set of species regenerating on a site. Climate and site factors are intricately intertwined, especially at the micro-climatological level.

Finally, it must be remembered the tree's regenerative interactions with pest systems. Pests produce periodic, sporadic, and/or continuous stress at all stages of tree reproduction and growth. Pests can act as major limitors of tree regeneration on a site.

STUDY METHODS

Sampling

The objective of this study was to sample oak forests for red and white oak regeneration in eastern Iowa and determine those factors most critically affecting the amount and distribution of oak regeneration.

Counties in which samples were to be taken were selected by the presence of more than 30,000 acres of commercial forest land on the basis of a 1974 Forest Service survey (Spencer and Jakes, 1980). One hundred thirty-three sample areas were examined. Table 4 lists the number of sample areas by county (Figure 3).

TABLE 4. List of the number of sample areas in each county

county	number of sample areas
Winneshiek	18
Allamakee	30
Clayton	29
Dubuque	16
Jackson	14
Van Buren	10
Lee	16

The definition used for identifying commercial forest land is any area producing, or capable of producing, crops

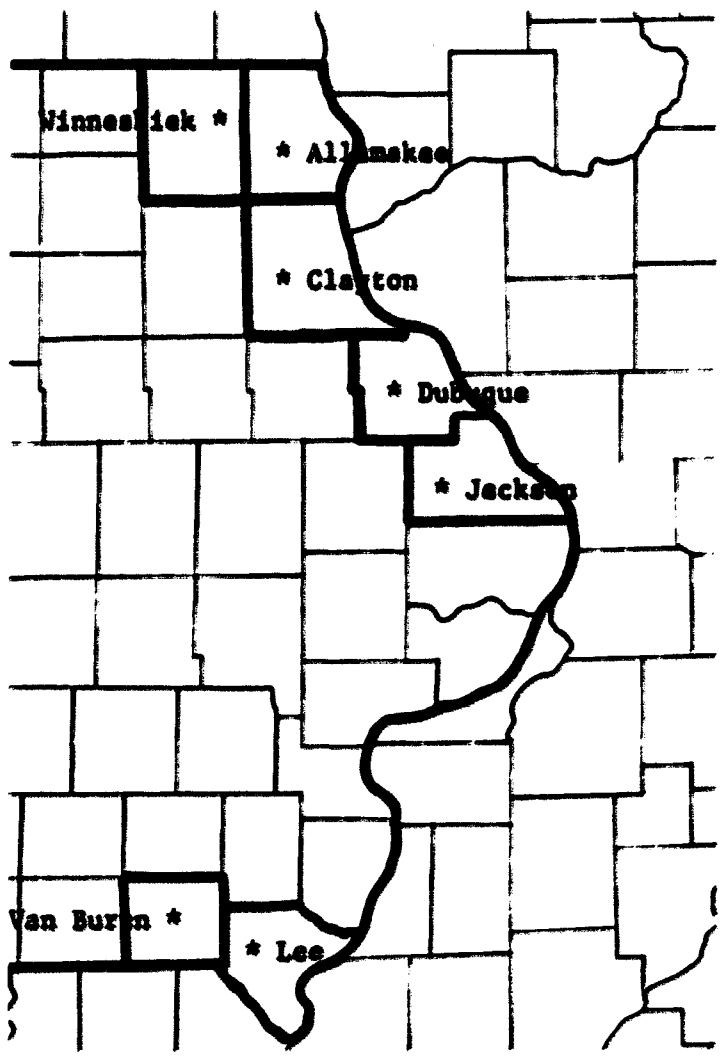

FIGURE 3. Location of Iowa counties sampled in this study

of industrial wood greater than twenty cubic feet per acre per year and which is not withdrawn from timber utilization by statute or regulation (Spencer and Jakes, 1980). Using counties with large commercial forest acreages minimized problems associated with sampling forest regeneration in more highly fragmented landscapes.

Samples were distributed to each county in proportion to the commercial forest acreage present. The samples were selected systematically in each county by overlaying a dot grid on USDA-Soil Conservation Service aerial photograph index sheets. The between-grid dot distance corresponded to 1.2 horizontal miles on the ground. Forest land was accepted if the land area was at least two continuous acres in size, was at least 120 feet wide along the shortest axis, had at least 15% of the ground surface area covered by visible living tree crowns, contained forest trees of any size, and was not developed for non-forest use or intensive recreation. Each sample must have met all criteria and definitions of forest land to be included.

Extra samples were identified at the time the original aerial photograph samples were picked. These back-up samples were selected in case the samples selected originally did not meet the study criteria. These back-up samples were picked randomly along the original selection

grid. In the field, when a sample area did not meet a criteria of the study, the first listed back-up sample was used if it met the study criteria.

Once the first sample was identified on a specific land-holding, additional samples were identified within the same land-holding. The criteria for identification of the additional samples were that they each meet all study criteria of the first sample, that they occur within the same land ownership, and that they occur on significantly different aspects and/or topographic positions. All samples on a landholding had, as well as could be ascertained, a uniform history of past treatment. Within the sample area, the site was as uniform as possible, while between samples, major differences occurred.

The other major concern in selecting samples was the presence of oak regeneration. The purpose of this study was to find where the oak was regenerating, therefore, only sites that had oak regeneration were sampled. A sample area with no regeneration could be the result of many factors. This study was interested in those factors responsible for oak regeneration, not the lack of regeneration.

The area of each sample covered one acre (0.4047 ha). Thirty mil-acre plots were identified systematically within each acre sample as points for determining variable values.

The sample contained a mil-acre plot orientation of five rows of six mil-acre plots, with the rows running perpendicular to the slope (Figure 4).

Each mil-acre plot was a 7.4-feet (2.26 m) diameter circle. Of the thirty mil-acre plots within the sample, four were systematically identified for additional measurement of variables. These four special mil-acre plots will be called hereafter "sample plots" or "sampled plots," as contrasted to all thirty mil-acres which will be referred to as "plots". Note that the four sampled plots are a subset of the thirty plots. To reiterate, the one-acre sample will be called the "sample area", the thirty mil-acre plots on the sample area will be referred to as "plots", and the four mil-acre plots identified for more intensive measurements and variable determinations will be referred to as "sample plots" or "sampled plots.". The sampled plots were systematically located (Figure 4). Each sampled plot was designated by the sample area number and a letter (a, b, c, or d).

Variables Measured

The following section will detail the variables observed or measured for each sample area.

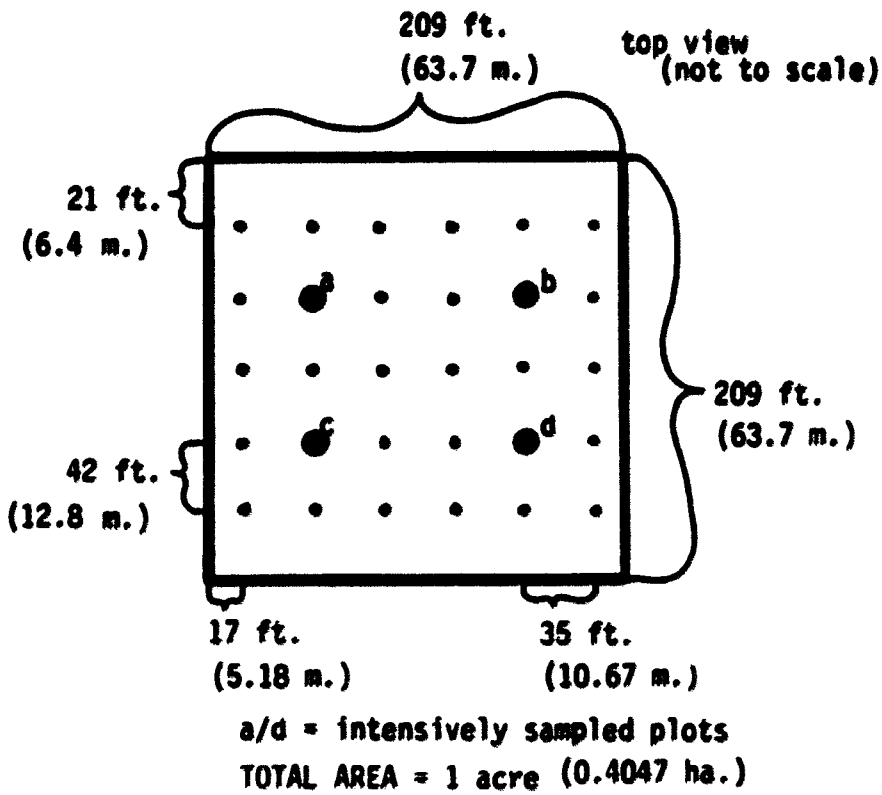

FIGURE 4. Graphical definition of a sample area and the relative positions of the sil-acre centers

Reproductive variables The reproduction on an area was determined by the presence of at least one seedling or sapling stem on each mil-acre plot summed over all thirty mil-acres. A seedling was defined as any living tree below 4.5 feet (1.37 m) tall relative to ground level. A sapling was defined as any living forest tree greater than 4.5 feet (1.37 m) tall relative to the ground and not greater than 4.0 inches (10.2 cm) diameter at 4.5 feet (1.37 m) above the ground. If a single or a number of seedlings or saplings were present on a mil-acre, that mil-acre plot was considered stocked for that species. If no seedling or sapling was present, the mil-acre plot was considered non-stocked for that species. The proportion of stocked mil-acre plots of a given species to the total number of mil-acre plots sampled, i.e., 30, provided a percent stocking over the sample area for that species.

Four mil-acres were identified for additional, more intensive data collection. Species identification, occurrence frequency, diameter at 2 cm above the ground, in seedlings, and 4.5 feet (1.37 m) above the ground, in saplings, and age in years at the level where diameter was measured were recorded. Diameter was recorded to the nearest millimeter and age estimated in years by cutting the tree down, then using a razor blade cut and hand lens for

age determination. The general overstory species of the sample area was recorded, and the specific overstory species in their respective vertical positions were recorded above each sample plot.

General variables Aspect is the dominant azimuth the site faces, if any. Aspect is an indirect measure of total energy input on the site. Variation in aspect can change temperatures and so change evaporation and evapotranspiration levels in the stand. Since the Iowa forests studied existed between the prairie parkland province and eastern deciduous forest province ecoregions (Bailey, 1981), the forest growth tends to change among the different aspects. Each aspect was measured using a liquid-filled compass on each sampled plot. The azimuth of all four sampled plots were averaged together to provide a composite aspect for the sample area. Corrections were made when azimuths were near zero so averages would be intuitively correct. For example, sample plots may have had azimuths of 2, 4, 1, and 359 degrees. The mathematical average would be 91.5, but the true average on a circular scale would be 1.5. Azimuths were determined to the nearest degree. Aspect measures were transformed for statistical analysis by the following formulas:

A = ASPECT - 202.5

SA= SIN (A/2)

The variable SA was used in the analysis for aspect (C. W. Mize, Department of Forestry, Iowa State University, Ames, Iowa, personal communication, 1984). The aspect values were sine-transformed to anchor the possible readings between 0 and 1, orientated along the axis between south by south-west and north by north-east. This axis was selected to more closely approximate total energy input to the site.

Slope is the vertical distance change over the horizontal distance change along a hillside perpendicular to a line connecting surface points of equal altitude. Slope is an indirect measure of water infiltration and erosion potential. Slope was determined by using a clinometer and recording the inclination to the nearest degree.

Topographic position is the specific location of an area relative to the flat topland and to the flat bottomland. Each position has differing characteristics and differing soil and water inputs and outputs. Erosion potential, infiltration, water holding capacity, and energy exchange patterns can vary over the topographic changes of the slope. Topographic position is closely tied with degrees of slope. Degrees of slope are relatively meaningless without knowledge of where the slope reading was taken on the topography. Topographic position was

determined for each sample plot. The position on the topography where the sampled plot fell was recorded following the definitions given in Figure 5.

Crown closure is an indirect measure of the photosynthetic surface and volume of plant material on the site. Generally, the larger the crown closure percentage over the site, the greater the water and nutrient requirements of the plants, but the lower surface evaporation on the site. Crown closure is the percentage of plant material visible in a given area of the canopy above the site. Crown closure is a direct measure of crown density and an indirect measure of crown competition and physiological state of the canopy. One minus crown closure is the percent of the sky viewed from the ground. Any vertical vector of the site above the sampled plot that is not interrupted by plant material is a part of the percent sky reading. The percent sky measure will be used in energy input determinations, and the crown closure measures will be used as crown competition factors. Crown closure, or the density of the canopy, was estimated by classifying the density of the tree canopy material above each sampled plot into 10% classes ranging from 0% crown closure for open sky to 100% crown closure for total crown coverage. The center of the crown closure measure was vertically above the

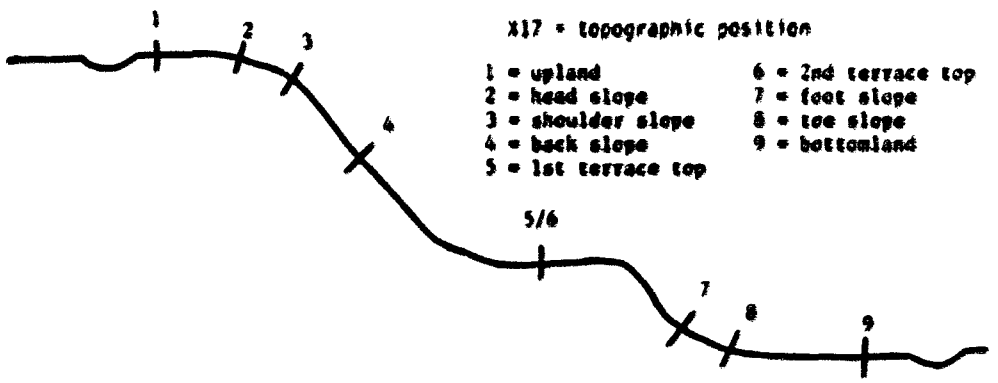

FIGURE 5. The coding definitions for the topographic position variable

sampled plot centers and covered 20 degrees of arc in diameter. Two crown closure measures were recorded; one measure was at ground level, and one was at 4.5 feet above the ground. These measures allowed for isolation of the effects of canopies above and below 4.5 feet. A third crown closure measure was calculated by subtracting the 4.5 level value from the ground level measure. This variable represents the added value the canopy below 4.5 feet has on the sampled plots.

Basal area is an indirect measure of overstory density and interference. Basal area is a density measure on the site based on tree size and number. The greater the total basal area of the site, the greater water and nutrient requirements of the trees, and probably the less water loss by surface evaporation. Basal area increment is a measure of the capacity of trees or stands to have produced xylem elements in the past. Production is partially controlled by genetics but is also a reflection of biotic, physical, and chemical factors of the site. The basal area of the trees on the site is the cross-sectional area of all the trees present on an acre at 4.5 feet above the ground. Basal area is an indirect measure of density and site quality if compared with age. Basal area was recorded using the center of each sampled area as the prism plot center. The basal

areas were determined using a prism with a 10 basal area factor. Total basal area, and red and white oak partial basal areas, were recorded for each sampled plot. The sample area basal areas were averages of the four sampled plot measurements. Three calculated variables were used to determine proportions of species' basal areas within total basal area. The calculated variables were white oak basal area over total basal area, red oak basal area over total basal area, and combined red and white oak basal area over total basal area on each sampled plot.

The total age and total height of three dominant or codominant red or white oaks were determined for each sampled area. Age was determined by using a hand-held, screw-type increment bore to remove a core from the tree and count the annual rings. The cores were removed from the tree at 4.5 feet above the ground. Total age was determined as core ring count plus four years to account for time to reach 4.5 feet (1.37 m) tall. Total heights were recorded for oak site index determinations and were estimated to the nearest foot with a clinometer.

Site index in this study was determined using oak site index curves by Wray and Thomson (1980). Site index is the height to which a tree will grow under forest conditions in 50 years. Site index determinations were made for three

dominant or codominant stems per sample area, and the average site index of all three trees was used for the sample area site index.

Cover density is the amount of forest understory occupied by different vegetation types. Cover measures provide an index of how fully utilized the site is and suggests the potential level of site interference associated with new reproduction. The greater the site utilization by other species, the less oak is expected to regenerate due to interference. Canopy area index is the decimal form of the percent coverage of the site due to the crown or leaf area of each vegetation component. Canopy area index yields that proportion of the plot covered by the canopy of that specific vegetation type. The cover density or canopy area index of the understory on each sampled plot was measured. The understory area, comprised of species less than one-half the total average height of the stand, was divided into seven cover types (Table 5). The percent of the sampled plot area covered by each cover class was determined in 10% intervals. Total combined areas can amount to more than 100% due to multiple canopy levels.

Litter depth to the nearest centimeter and litter type were determined in the center of each sampled plot. Litter accumulation and breakdown is important to nutrient

TABLE 5. Understory cover type classes measured for each sample area

red oak regeneration
white oak regeneration
other tree species regeneration
shrubs
forbs
grasses
non-occupied space

recycling, water infiltration, and water holding capacity in the soil. Litter depth was measured from the dominant litter surface to the mineral soil level. Litter was typed according to the following classification:

mor - litter is unincorporated into the mineral soil

moder - intermediate type

mull - mixed litter-mineral soil transition zone

none - no forest floor development

Litter continuity over each sampled plot was recorded as either continuous or spotty. The spotty designation was used to show broken, disturbed, or eroded litter layers and was invoked where mineral soil and litter site-coverage was of roughly equal proportions.

Light variables Light is difficult to measure accurately due to spacial and temporal variations in

intensity and quality. The variation in quality probably has little differential affect on photosynthesis because the leaves of most terrestrial plants absorb the same wavelengths of light. An average leaf is a selective filter with an extinction factor of 95% or greater across the leaf in wavelengths utilized by chlorophylls and carotenoids. There seems to be few differences in the basic wavelength uptake between leaves from different species (Loomis, 1965). The relative amount of light available at some point on the forest floor depends upon canopy coverage due to foliage and branch interception.

The temporal pattern of light at different points above the forest is roughly the same over uniform areas. The relative amount of radiant energy reaching a given point in the forest is inversely correlated with the density of foliage between that point and the sky. Comparisons of foliage densities within a single area are equivalent to comparisons of light intensities (Horn, 1971).

Since light is critical to tree maintenance and growth, the shading of trees and understory plants in the forest should profoundly affect the growth of regeneration. If the relative amount of light beneath the canopy and the light required by seedlings in the understory are determined, prediction of species regeneration can be attempted. If

none of the regeneration has atypical requirements for minerals, moisture, and other site qualities, predictions should correspond to knowledge about light input on the site, past practices, and interference.

Any measure of light on the forest floor, regardless of how accurate and/or physiologically appropriate, confounds root and shoot effects since the foliage demands water, nutrients, and growth substances. The initial tendency of shade on many tree seedlings is to decrease the relative growth of the root system, and so lower the ability of the roots to compete with each other in an area (Eliassen, 1971; Horn, 1971). Root competition and shoot competition are not independent and distinct physiologically or ecologically. In this study, the total effect of the canopy is measured rather than the effect of shading alone.

In a general sense, for regeneration, light at ground level must be above the light compensation point. The light compensation point of most plants in the forest is 2-3% of full sunlight. Light compensation is a point where respiration expense of fixed carbon in the plant is just balanced by fixation of carbon by photosynthesis. Due to the physiological effectiveness of the photosynthate production mechanism in the plant, the maximum photosynthate production rate levels out in light that is about 20% of

full sunlight. This is called the light saturation point (Daniel et al., 1979). Light at ground level can become significantly related to regeneration where the light quantity falls between the light compensation point and the light saturation point. Light measures can show relative species differences in an understory position.

Light through the canopy to the ground is a negative exponential function of leaf density. The total light interception on the site is proportional to the horizontal projection area of leaf, branch, and stem material. Shading of one leaf upon another depends upon the distance between leaves. Direct light is blocked for 50-70 effective leaf diameters below a leaf. Diffuse light is blocked for one effective leaf diameter below a leaf. Effective leaf diameter is a method of modeling the light extinction patterns of the leaves.

Effective leaf diameter is the diameter of the largest circle that can be inscribed in the leaf. The larger the effective leaf area, the greater the self-shading that will occur, and the less photosynthesis that will occur (Horn, 1971). Three field-measured effective leaf diameters were recorded on each sampled plot. They were the average effective leaf diameter in the vertical 0 to 4.5 foot (0-1.37 m) zone, the 4.5 foot (1.37 m) to the canopy-top

zone, and the 0 to the canopy-top zone. Effective leaf diameters were estimated by measuring a number of leaves in each zone. A calculated variable was developed by adding the 0 to 4.5 foot zone value to the 4.5 feet to canopy-top zone value, then dividing by 2 to produce an "average" value.

The model used to describe light characteristics in the sample areas, from the ground to canopy top, is from Horn (1971). The model estimates light passing through the canopy of the forest. Horn utilized the model to provide information on tree crowns. The principles of his study have been expanded in this study to encompass light penetration throughout a vertical portion of the forest above the sample plots. Descriptions, assumptions, and proofs of Horn's work will not be given here. Reference should be made to his 1971 monograph. The model uses the effective leaf diameter and the percent open sky above the site as data inputs. The major assumption made is that the proportion of open sky above a site is negatively proportional to leaf density. The model has been tested and shown to be accurate in two temperate broadleaf forests, one temperate conifer forest, and one tropical forest (Horn, 1971).

Below are given the definitions of terms used in the equations to produce the variables for each canopy zone:

model equations:

ELA= -(log s)

ANL= -(log s) / pi r ^{2}

where:

r = average effective radius of the leaves
from effective leaf diameters
over the canopy zones

s = percent clear sky or 1-crown closure
for each canopy zone

log = natural logarithms to base e (ln)

ELA = effective leaf area (one value for
0-canopy-top zone and one for 4.5
feet-canopy-top zone)

ANL = average number of leaves present above a
point of ground (one value for 0-canopy-top zone
and one for 4.5 feet-canopy-top zone)

The information developed here will provide light competition comparisons among different sites with varying levels of oak regeneration. The light determinations will be composed of two variable sets, one set characterizing the light available between 4.5 feet above the ground and the

top of the canopy, and the other set characterizing the light available between the ground surface and the top of the canopy. The two variable sets can suggest, for a particular site, at what level the light is being most limited, the understory below 4.5 feet or in the canopy.

The incoming direct and diffuse radiation on a site was estimated on a relative basis by calculating the direct beam radiation impinging on a site at five times during the day. The times were 8 am, 10 am, 12 noon, 2 pm, and 4pm (TST). The direct beam energy input was estimated on a relative basis at each of these times for one day every month. The sum of the five calculations for each day was used as the relative direct radiation input level. A correction for diffuse solar radiation was included in the direct beam estimate for a site. The basis of the calculations all come from the Smithsonian Meteorological Tables (List, 1965). The basic formulae for direct and diffuse radiation input to a site are from Shaw (1983) and are given below:

$$TDBR = TDBRn(\cos B \cos(90-a) + \sin B \sin(90-a)\cos(z - d))$$

$$Rdt = TDBR * C$$

where:

TDBR = total direct beam radiation input on a site

TDBRn = total direct beam radiation input on a normal surface (Table 6)

B = degrees of slope

a = solar altitude

z = solar azimuth

d = azimuth of slope

Rdb = total direct and diffuse radiation input on a site

C = relative diffuse radiation component

The relative total direct beam radiation input on a normal surface (TDFRn) for each date is given in Table 6 as well as the relative correction value for diffuse radiation input for each month used for correcting the total direct beam radiation input for a site (TDBR).

TABLE 6. The relative amount of total direct beam radiation input on a normal surface (TDBRn) for each calculation date and the associated correction value for diffuse radiation

date	relative TDBRn	diffuse radiation correction
March 21	13.0	1.45
April 16	15.0	1.50
May 21	18.0	1.47
June 22	20.0	1.44
July 24	21.0	1.38
August 28	20.0	1.35
September 23	16.0	1.38
October 20	14.5	1.29
November 22	10.5	1.30
December 22	8.5	1.29
January 21	10.0	1.27
Febuary 23	12.5	1.32

The solar altitude and solar azimuth used for the five calculations per day per month are for 42 N latitude and are given in Table 7.

Several combinations of monthly values were used as variables. One variable included all months for a relative total radiation input to a site. A second variable included the relative total growing season radiation input to a site, which included the monthly values from April through September. The third relative radiation variable included those monthly values from the spring warm-up period, which included the months of Febuary through May. The final variable included was for the period of time when photosynthesis was maximized, which included the months of May through July. Individual monthly values were originally put into the regression models for regeneration but were found not to be as strongly correlated with regeneration levels as the composite variables.

Soil variables The number and type of soil variables to measure were determined on the basis of a survey of 30 different species-site multiple regressions from the literature since 1970. Due to time and money constraints, it was determined that only those variables from the survey shown to have the highest probabilty of affecting regeneration would be included in this study.

TABLE 7. The solar altitude and solar azimuth used for the five calculations per day per month from the reference tables for 42 N latitude (List, 1965)

date	TS time	solar altitude	solar azimuth
March 21-	8	21.5	112.0
Sept. 23	10	39.5	139.5
	12	47.5	180.0
	2	39.5	220.5
	4	21.5	248.0
April 16-	8	28.5	104.0
Aug. 28	10	48.5	131.5
	12	57.5	180.0
	2	48.5	228.5
	4	28.5	256.0
May 21-	8	35.5	95.0
July 24	10	56.5	122.0
	12	67.5	180.0
	2	56.5	238.0
	4	35.5	265.0
June 22	8	37.5	91.0
	10	59.0	117.5
	12	61.5	180.0
	2	59.0	242.5
	4	37.5	269.0
Oct. 20-	8	14.0	118.0
Feb. 23	10	31.0	144.5
	12	37.5	180.0
	2	31.0	215.5
	4	14.0	242.0
Nov. 22-	8	6.5	125.0
Jan. 21	10	21.5	149.5
	12	28.0	180.0
	2	21.5	210.5
	4	6.5	235.0
Dec. 22	8	4.0	127.5
	10	18.5	151.5
	12	23.5	180.0
	2	18.5	208.5
	4	4.0	232.5

Variables utilized from the survey were the most common soil and nutrient variables affecting tree growth from studies of forested sites across the United States and Canada (Alban, 1974; Bowersox and Ward, 1972; Bowersox and Ward, 1977; Broadfoot, 1969; Brown and Lowenstein, 1978; Dumanski et al., 1973; Esu and Grigal, 1979; Fralish and Loucks, 1975; Geyer et al., 1980; Gilmore, 1976; Graney and Ferguson, 1971; Graney and Ferguson, 1972; Grigal and Arneman, 1970; Hannah, 1969; Heger, 1971; Klinka et al., 1980; Leary, 1975; Nader, 1976; Naeglin and Nelson, 1970; McKee, 1977; McKee and Shoulders, 1974; McQuilkin, 1976; Nogren and Colph, 1972; Munn and Vimmerstedt, 1980; Neseth and Davey, 1974; Page, 1976; Powers, 1980; Shoulders and Tiarks, 1980; Sprackling, 1973; Wikum and Wali, 1974).

Table 8 lists all the variables from all the regression equations reviewed. All variables were significant in accounting for variation in each sampled species on a given site. Several variables are clearly region- or species-specific, while other variables occur repeatably in regression equations. By recording the number of instances where a specific variable was used and significant, more information can be assessed about forested sites region-wide.

TABLE 8. List of the variables found in the surveyed multiple regression formulas to be related to tree growth (grouped by general interest areas)

CHEMISTRY - pH of the A soil horizon, pH of the C soil horizon, cation exchange capacity, base saturation, hue, value, and chroma.

BIOTIC - organic matter, carbon to nitrogen ratio of soil organic matter, age of trees, solar irradiation, exposure to wind, and growing space.

PHYSICAL - thickness of humus layer, thickness of A horizon, thickness of B horizon, depth of B horizon, depth of A plus B horizon, depth to gleying, depth to mottling or impervious layer, depth to bedrock, depth to water table, presence of a fragipan, bulk density of the soil, bulk density of the A horizon, bulk density of the B horizon.

TEXTURE - silt plus clay in the A horizon, silt, clay, sand, stones, Silt A, clay in the A horizon, sand in the A horizon, coarse fragments in the A horizon, silt in the B horizon, clay in the B horizon, sand in the B horizon, coarse soil fragments in the B horizon, coarse soil fragments in the B and C horizon.

ELEMENTS - sodium, phosphorus, iron, nitrogen, potassium, magnesium, calcium, manganese, zinc, soluable salts, iron phosphates.

WATER - moisture availability, field capacity, rainfall, pore space.

SITE - elevation, slope position, slope, aspect, distance from ridge top, and distance from sea.

Table 9 is a list of the soil variables found to be important in hardwood growth. The five variables listed most often as significant for hardwood tree growth were calcium, phosphorus, magnesium, moisture availability, and pH of the A horizon. These variables suggest that low pHs, water, energy, and photosynthesis functions are most limiting in hardwoods. Nitrogen was also a major factor in hardwood growth (Alban, 1974; Bowersox and Ward, 1972; Bowersox and Ward, 1977; Broadfoot, 1969; Fralish and Loucks, 1975; Geyer et al., 1980; Gilmore, 1976; Maeglin and Nelson, 1970; McKee, 1977; McQuilkin, 1976; Munn and Vimmerstedt, 1980; Nikum and Wali, 1974).

Upon identification of the variables with single linear correlation signs on hardwood sites, as the pH of the A horizon, nitrogen, depth of the A horizon, and slope increase, the greater will be the expected hardwood growth. Increasing the amount of sand in the A horizon decreases potential hardwood growth.

From this survey of other soil-site studies, the following soil variables were identified to be either measured in the field or determined in the lab: calcium (Ca), phosphorus (P), magnesium (Mg), soil texture and pH of the A horizon, nitrogen (N), pottassium (K), and slope aspect.

TABLE 9. List of important variables over all hardwood sites, with rank based on number of citations or uses of the variable in the literature

variable	sign of correlation	relative numeric ranking
Ca	+-	1
P	+-	2
Mg	+-	2
Moisture availability	+-	3
pH A	+	4
N	+	5
K	+-	6
Aspect	+-	6
Organic matter	+-	7
Clay A	+-	7
Silt + Clay A	+-	7
Depth A + B	+-	7
Depth A	+	7
Elevation	+-	8
Slope	+	8
Sand A	-	9

The soil was sampled in the center of each sampled plot using a bulk density sampler (slap-hammer type) to take a 344.77 cubic centimeter sample of the top 4 inches (10.16 cm) of the mineral soil. The samples from all four sampled plots were put into a 4 mil thick polyethylene bag and sealed with a wire tie. The sample bags were then stored for as much as two months. The bags were then opened and the contents examined. The large pieces of stone and root material were removed, if any. The sample was then mechanically broken up into small pieces using a wooden

mallet and a rolling pin to pass a 20 mesh sieve (zinc-coated steel wire with 20 wires per inch in both directions with wire size of 0.038 inches) and put into a brown, kraft paper bag and stored for 2 months at approximately 67 degrees Fahrenheit and 30% relative humidity. The sample material not passing the mesh was saved for coarse fraction determinations. During sieving, the soil was mixed by rolling the soil over on the sieving board. After sieving, the soil was mixed by shaking the sample bag. All soil measures were taken from this mixed soil sample. This mixing technique was tested by adding small white sand particles to a soil sample. The sand was visibly well-mixed with the soil after this procedure.

Bulk density is the weight of soil solids per unit volume of total soil sampled. Bulk density of the soil varies according to the degree of compaction. The higher the bulk density, the slower the infiltration rate of water. Bulk densities will also affect root penetration ability. Bulk density determinations followed the American Society of Agronomy standards (Blake, 1965). A subsample of the bulk density sample was oven-dried at 105 degrees Celsius, then weighed to determine sample moisture content. Bulk density is the oven dried weight of the sample over the field volume. The field volume of each sample was a multiple of 344.77 cubic centimeters.

Soil pH is a complex variable. Generally, high pH represents unfavorable conditions due to deficiencies of essential elements, and low pH represents toxicity by metals. Soil pH fluctuates seasonally in many soils (i.e., one pH unit change). The pH scale serves as a measure of the negative log of the hydrogen ion concentration, and so has a major effect on nutrient status in the soil. Soil pH is an indirect measure of water quality. Each sampled plot had soil pH determined by the American Society of Agronomy standard methods for pH determined in water (Peech, 1965). Each sample area had one value of pH that was an average of the four values determined from the sampled plots.

The soil pH was recorded to the nearest tenth of a unit on an electronic pH meter. The meter was in a plexiglass case to minimize temperature fluctuations from air circulation in the room. The meter was standardized using two sets of a commercially produced buffer solutions. The standards were referenced at pH 4 and at pH 7. A 20 gram subsample of soil was taken from the bulk density sample that had been sieved to pass a #20 sieve. The subsample was taken by multiple divisions in a subsampler to near 20 grams and a chemical spoon was used to remove material from the top of the sample to bring the sample weight to 20.00 grams. The 20.00 gram sample was put into a 50 ml white paper cup

that was unwaxed and 20 ml of distilled water were added. Paper cups were used because of convenience. After 6 hours the pH in paper cups compared to glass beakers varied one-tenth of a pH unit for the same soil sample. However, after only one and one-half hours for each measure, paper cups did not produce measurable accuracy problems. The mixture was stirred 2 times at 10 minute intervals over the next 30 minutes. The mixture was then left to settle for one hour. The measures were then taken with the electrode poles going across the soil-water interface. The pH results are "soil pH measured in water".

The soil moisture index used in this study is from Johnson (1975) and P. S. Johnson (USDA-Forest Service, Columbia, Missouri, personal communication, 1984). The journal article cited has several typographical errors in it that are here corrected. The errors occurred in the signs and constants in the various formulae. Contacting Dr. Paul Johnson, USDA-Forest Service, Columbia, Missouri is suggested for insuring complete corrections. The soil moisture index (SMI) was derived from the work of Stoeckeler and Curtis (1960) on moisture contents beneath various species and on various slopes in the Wisconsin driftless area. The formulae are for a transformation of aspect and the calculation of SMI based on slope position. The formulae follow:

A = (cos (45 - azimuth in degrees)) ÷ 2

SRI = a + b (A)

where:	value of a	value of b
lower slopes	0.072	0.096
middle slopes	0.032	0.094
upper slopes	0.040	0.082

Generally, the better water availabilities occur away from the midslope area and away from the higher direct beam radiation inputs.

Soil texture is the percentage, by weight, of three size classes in soil smaller than 0.5 mm in diameter. Soil texture has a considerable effect on water holding capacity and on cation-exchange capacity. Fine textured soil has more surface area for holding water and nutrients compared to coarse textured soils. The amount of the sand, silt, or clay particle size class in a soil can determine some of the water-soil-root interactions present. Texture was determined using the hydrometer-column method following the American Society of Agronomy standards (Day, 1965). The bulk density soil sample had been mixed by seiving through a 20 mesh seive and then by hand. A subsample was then removed by multiple divisions in a subsampler for texture

determinations. Using graphical procedures, the percentages of sand and clay were recorded.

The texture determination procedure began with the preparation of a sodium hexametaphosphate solution, required to keep the soil particles separated and in suspension. The sodium hexametaphosphate solution was made by dissolving 50 grams of the commercial product "Calgon" (Calgon Commercial Division, 7405 Page Ave., St Louis, MO., 63133) in distilled and filtered (to remove organics) water, then diluted to a volume of 1 liter.

Forty grams of soil were taken from the soil sample for analysis, and forty grams of soil were taken for oven drying so moisture content could be determined. The oven dry sample was dried at 105 degrees Celsius until no weight change occurred on two successive measures. Drying could be expected to be complete in 36 hours.

The 40 gram soil sample was then placed in a 600 ml beaker with 100 ml of the "Calgon" solution and 400 ml distilled water. The mixture was allowed to sit for 10 minutes. The mixture was then transferred to a stainless steel mixing container and mixed for five minutes at 6200 rpms in an American Instrument Co. mixer with a 1 cm radius blade. Immediately after mixing, the suspension was transferred to a standard settling column and distilled

water added to the 1 liter volume level. All measurements were made in a room where temperature did not fluctuate greatly and there was no air circulation. Distilled water for this procedure was stored in a large glass container in the same room so the water would be in temperature equilibrium with the air temperature.

The suspension temperature was then recorded. The settling column was then sealed and completely inverted eight times while swirling the contents in a counter-clockwise direction. Immediately after setting the column down and removing the stopper, the time was recorded and a timer started. A drop or two of amyl alcohol was usually needed to eliminate foaming of the mixture. The addition of the alcohol if added to the column in this way caused no significant change in readings. Amyl alcohol should not be added before mixing or inverting since the surface tension of the air bubbles will be destroyed and the small bubbles produced will affect the bouyancy of the hydrometer.

The hydrometer to be used was checked for accuracy by measuring a column of water and a column of the "Calgon" solution. If the hydrometer read zero in the first situation and five in the second situation, and the reading could be accurately read on the hydrometer scale, then that hydrometer was acceptable for use. Several hydrometers were

checked for accuracy at the same time to insure precision in the measures if the original hydrometer was broken. All hydrometers should be checked before use since significant differences of up to 2 grams per liter were found to occur in readings of the same columns by different hydrometers.

As soon as possible after setting down the column, the hydrometer was lowered carefully into the column to minimize turbulence from the hydrometer. Hydrometer readings were taken at 30 seconds and at 1, 3, 10, 30, 90, 270, 480, and 720 minutes. The hydrometers were removed after each reading except the first two and carefully rinsed off as they were being removed from the column. The hydrometer reading taken is the R value. The R value is the concentration of solids in suspension measured in grams per liter. To determine the percent sand, silt, and clay in the sample required graphical techinques. The formulae for graphing and determing the soil fractions are:

```
C=R-RL
P=(100)*(C/40)
SP=(-0.2761 * (R) + 49.2997)*(-0.0285 * (TEMP) + 1.8263)
X=SP/(TIME ** 0.5)
XL=LOG10(X)
```

where:

from reccrded measures-

TEMP = temperature (C)

RL = standardized hydrometer reading of sodium hexametaphosphate solution

R = hydrometer reading from column

TIME = time (MIN)

from calculations-

C = concentration in suspension (GRAMS/LITER)

P = summation percentage

X = particle size (MICRONS)

SP = sedimentation parameter from R-value (-0.2761 * R + 49.2997) (R-square = .999)

XL = LOG (BASE 10) of X

CORV = correction for water viscosity (-0.0285 * TEMP + 1.0263) (R-square = .999)

A plot can then be made of P*XL where the clay portion is less than 0.301 microns and the sand portion is greater than 1.699 microns.

Other soil variables collected were the amount of potassium, magnesium, and calcium present in the A soil horizon as determined by an atomic absorption spectraphotometer. Phosphorus and nitrogen levels were determined for the A soil horizon by a modified Technicon Auto Analyzer II system based on photometric determinations of specific reactions. Coarse fraction determinations were

the portions of the sample soil left behind on the #20 sieve. Activity ratios of nutrients in the soil were used to give a more accurate accounting of usable nutrient quantities in soils with strong cation exchange capacity. The cation concentrations were inserted into activity ratios with the cation concentration over the combined concentration of calcium and magnesium (Beckett, 1972; A. M. Blackmer, Department of Agronomy, Iowa State University, Ames, Iowa, personal communication, 1984). More detailed information about each variable follows.

Soil extractions for nutrient analysis were made with a Bray I solution. Bray I is 2.6 ml of concentrated hydrochloric acid (HCl) and 1.4 grams ammonia-flouride per liter of distilled water. The soil for extraction had passed a #20 mesh sieve. Four grams (4.00 g.) of subsampled soil were put into 250 ml flasks with stoppers. Then, 40 ml of Bray I solution was added. The flask was stoppered and shaken for 10 minutes on a reciprocating shaker (Burrell wrist-action shaker). The flasks were then unstoppered and the contents filtered through #42 Whatman filter paper and put into prewashed plastic vials. The liquid samples were then diluted with a manual diluter for use with the atomic absorption spectrophotometer and the phosphorus determinations.

The soil cations of potassium, calcium, and magnesium were quantified on a Perkin-Elmer 272 atomic absorption spectrophotometer with an air-acetylene flame. The machine has the capability to read out directly in parts-per-million, once standardized. For potassium, 1250 ppm sodium were added to the final measured solution to prevent wildly fluctuating readings. The light slit was set at 2.0 nm. and the wavelength was set at 766.4 nm. The lamp energy used was 12 milli-amps (mA). Dilutions were used to lower the concentration of potassium in the sample to between 1 ppm and 5 ppm. The dark red filter was used in the machine for the potassium determinations.

Magnesium samples were diluted to contain between 0.1 ppm and 1.0 ppm of the element. The final dilution also contained 1250 ppm lanthanum to prevent wild fluctuations in readings. The light slit was at 0.7 nm. and the wavelength was set at 285.5 nm. The lamp energy was set at 15 mA. The samples were periodically shaken to insure proper readings.

Calcium concentrations were determined with solution dilutions between 1 and 10 ppm of calcium with 1250 ppm of lanthanum in the final sample solution. The light slit was set at 0.7 nm. and the wavelength set at 423.0 nm. The lamp energy was set at 19 mA. The samples were periodically shaken to insure proper readings.

Phosphorus content in the A soil horizon was determined using the Bray I extraction solution from the atomic absorption spectrophotometer procedure. The Bray I sample solution was measured on a modified Technicon Auto Analyzer II, using Industrial Method number 327-74W (March, 1975) from Technicon Instruments Corporation, Tarrytown, New York 10591 by a laboratory technician within 2 days of extraction.

Total nitrogen in the A soil horizon was determined by acid-selenium digestion, then measured in a modified Technicon Auto Analyzer II, using Industrial Method number 325-74W (March, 1975) from Technicon Instruments Corporation, Tarrytown, New York 10591. A Lachat Instrument Co. DG-1 block digester, running at 390 C was used for the analysis. A 0.500 gram soil subsample was used for the determination. A sulfuric acid-selenium solution was used for extraction. The solution was prepared by dissolving 12 grams of selenium in a full 9 lb bottle of reagent grade sulfuric acid. The sample was placed into a block digestion tube, then 10 ml of the sulfuric acid-selenium solution were added and allowed to set 14 hours. The sample tube was then charred for 10 minutes at 390 C on the block. The sample was then removed from the block and allowed to cool 15 minutes. Hydrogen peroxide (30% reagent grade) was then

carefully added to the sample in 10 ml increments until a light colored liquid remained in the sample tube. Approximately 10 ml of peroxide were required in most samples for this oxidation. The peroxide was added fast enough for a strong reaction to occur. The sample tubes were then placed back on the block for 1 hour. At the end of one hour, the remaining liquid was clear and allowed to cool.

The sample was diluted with distilled water to 75 ml and the digest tube inverted 2 times to mix the contents. During this procedure, five sets of standards were run with the samples, using glycine as a nitrogen source. The glycine was directly weighed into the digestion tubes. All samples were then allowed to settle for 2 days, when an aliquot was taken from the clear portion of the liquid. The aliquot was put into a sample vial on the sample siphoning portion of the automatic analyzer. The measurements were completed by a lab technician and returned within two days. Multiple samples of the same soil and standards were included to determine precision and accuracy of the technique. The technique was found to be precise and accurate.

Site descriptions The past-use history of each sampled area was determined from observation, from

discussion with the landowner and/or land tenant, if present, and from questioning officials from county government and the federal USDA-ASCS offices. A notebook was kept on the descriptions of each sampled area and the general impressions of the surveyor concerning the forested site.

Principal Component Data Compression

The scores of principle components were used as composite variables for the soil, nutrient, and climatic data because they accounted for the full distribution of the data along separate, statistically independent dimensions while allowing for a fewer number of variables to be carried in the analyses. In a linear model system, the eigenvector of the largest eigenvalue is the greatest dimension of spread in the data. Each proceding eigenvector-eigenvalue denotes the next greatest dimension spread of the data cloud orthogonal to the preceding eigenvectors-eigenvalues. With each additional principal component determined, the remaining data spread axes become smaller and may only account for little of the total data cloud spread (Johnson and Wichern, 1982). The scores of the principal components that composed the major proportion of data variance were

included as variables in the multiple regressions. The software used to calculate principal components was SAS-PRINCOMP (Ray, 1982a and 1982b; Sarle, 1982b).

Principal component analysis was used on the soil and nutrient variables to summarize the very complex data and to more accurately reflect, by way of increased R-squares in later analyses, the relationship between soil-nutrient variables and regeneration. The soil-nutrient data were composed of the 20 variables in Table 10 which were summarized into the first 12 principal component scores. The first twelve principal components were utilized, even though some of the higher dimension principal components accounted for relatively small data cloud variance, for two reasons. The first reason was that all principal components used had dominate loading factors identified from the literature as associated with forest productivity (Table 9). The second reason was that a preliminary stepwise multiple regression was completed using all soil and nutrient principal components, and a number of the first twelve principal components were statistically significant in the models.

Each score utilized in this study could have had up to three elemental concentration inputs for each element measured. The reason for the three elemental measures,

which were the concentration in parts-per-million, the negative log of the concentration, and the activity ratio of the element, was that the three measures were accurately represented or accounted for the variance in the data than any one measure alone. Separate analyses were produced to determine the predictive value of each of the three measures and the one combined group of measures. Once the principal component scores were determined in the four separate test analyses, they were put into a stepwise multiple regression with the red oak, white oak, combined oak, sugar maple, and total regeneration stocking data. The results showed that the scores from the combined group of measures better accounted for data variance than the individual elemental measures. On the basis of this test, the scores from the principal component analysis of soil and nutrient data, which included the composite elemental measures, were used in subsequent multiple regressions. The soil and nutrient variables included in the principal component analysis are given in Table 10. The soil and nutrient principal component analysis is summarized in Table 11.

Of the twenty variables included, the first 12 principal components accounted for 99.8% of the variation in the data. The scores from the first 12 principal components were included in the data set as multiple-regression,

TABLE 10. Soil variables included in the principal component analysis

soil variable (variable code)
clay (s1)
sand (s2)
bulk density (s3)
coarse soil fractions (s4)
potassium ppm (s5)
magnesium ppm (s6)
calcium ppm (s7)
pH (s8)
phosphorus ppm (s9)
total extractable nitrogen ppm (s10)
soil moisture index (s11)
pCa (s12) [1]
pMg (s13) [1]
pK (s14) [1]
activity ratio of K (s15) [2]
activity ratio of Ca (s16) [2]
activity ratio of Mg (s17) [2]
activity ratio of H (s18) [2]
cosposite ratio of nutrients = pCa/pMg/pK (s19)
composite ratio of nutrients = (Ca/Mg/K) all ppm (s20)

[1] -LOG(1/(X ppm/1,000,000)).

[2] pX-(0.5*(LOG(1/((Ca ppm/1,000,000)+(Mg ppm/1,000,000))))).

cosposite variables. The soil variables, individually or in combinatien, did not account for as much variation in the data as did their principal component scores.

Principal component analysis was alsc used to simplify climatic data. The variables within the climatic variable grcup are listed in Table 12.

TABLE 11. Soil and nutrient principal component analysis with variables from Table 10

principal component	eigenvalue
NUTR1	7.44
NUTR2	3.11
NUTR3	2.06
NUTR4	1.71
NUTR5	1.28
NUTR6	1.04
NUTR7	0.85
NUTR8	0.75
NUTR9	0.60
NUTR10	0.44
NUTR11	0.34
NUTR12	0.26

variable code	eigenvectors 1	2	3	4	5	6
s1	.16	.09	.04	-.50 *	-.06	.20
s2	.03	-.01	.27	-.06	.65 *	-.16
s3	-.17	.19	.08	-.27	.25	.19
s4	.16	-.06	.23	-.15	.35 *	.18
s5	.20	-.09	-.39 *	-.15	.14	.09
s6	.32 *	-.05	.25	-.13	-.02	.01
s7	-.04	-.55 *	.05	-.10	-.06	-.01
s8	.24	-.05	.15	.38 *	-.09	.46 *
s9	.09	-.05	-.36 *	.38 *	.16	-.19
s10	.22	-.06	.01	.16	.28	-.24
s11	.03	-.14	.06	.28	.35 *	-.03
s12	.04	.55 *	-.04	.12	.04	.01
s13	-.32 *	.04	-.25	.06	.13	.20
s14	-.28	.09	.40 *	.15	-.08	-.09
s15	-.27	-.03	.43 *	.11	-.10	-.09
s16	.11	.53 *	.02	.09	.03	.01
s17	-.33 *	-.03	-.24	.04	.12	.21
s18	.24	-.07	.16	.37 *	-.09	.46 *
s19	.36 *	.09	.02	-.09	-.01	-.06
s20	-.25	-.03	-.04	-.01	.26	.45 *

*Major loading factors.

Table 11. (continued)

variable code	eigenvectors 7	8	9	10	11	12
s1	.14	.02	.36 *	.42 *	-.10	.54 *
s2	-.42 *	.09	.18	-.23	-.41 *	.17
s3	-.04	.65 *	.06	-.02	.52 *	-.25
s4	.08	-.24	-.76 *	.12	.22	.19
s5	-.01	.02	.03	-.14	-.02	-.09
s6	.06	.01	.01	.22	-.20	-.36 *
s7	-.04	.08	.01	.03	.01	-.05
s8	-.15	.09	.07	-.10	.04	.10
s9	-.17	.37 *	-.16	.66 *	-.09	.09
s10	-.08	-.44 *	.42 *	.16	.62 *	-.01
s11	.83 *	.18	.14	-.11	-.10	.08
s12	.05	-.07	-.03	-.03	-.04	.02
s13	-.03	-.12	.01	-.05	.02	.19
s14	.01	-.01	.03	.19	.02	.06
s15	-.01	.01	.04	.22	.02	.03
s16	.06	-.07	-.03	.03	-.08	-.06
s17	-.03	-.12	.01	-.04	.02	.17
s18	-.15	.09	.08	-.09	.04	.09
s19	.04	.04	-.01	.01	-.07	-.22
s20	.02	-.30	.14	.32 *	-.22	-.58 *

PREDOMINANT LOADING OF PRINCIPAL COMPONENTS	
NUTR1	= +magnesium
NUTR2	= -calcium
NUTR3	= -potassium and -phosphorus
NUTR4	= -clay, +pH, and +phosphorus
NUTR5	= +sand, +coarse soil fractions, and +SMI
NUTR6	= +pH
NUTR7	= -sand and +SMI
NUTR8	= +bulk density, -nitrogen, and +phosphorus
NUTR9	= +clay, -coarse soil fractions, and +nitrogen
NUTR10	= +clay and +phosphorus
NUTR11	= -sand, +bulk density, and +nitrogen
NUTR12	= +clay and -magnesium

The total number of climatic variables included in the principal components analysis was 23. Each was collected following the technique of Rauscher (1984) by laying a scaled map transparency, on which the sample areas are identified, over the climatic maps having iso-climatic lines of variable gradients. The variables were determined by interpolation for each sample area. This procedure produced a good general climatic breakdown of the sample areas. The first three principal components accounted for 97.6% of the variation in the data. The scores of the first three principal components were used to summarize climatic variables. The climatic data principal component analysis is summarized in Table 13.

The climatic principal components were included if they provided for a large proportion of the data variance (i.e., CLIMATE1 and CLIMATE2) or if they contained a single, large loading factor coeffecient (i.e., CLIMATE3). The trend in the distribution of the first principal component over the sampled counties followed roughly the increasing temperatures over the year from north to south, coupled with a general increase in precipitation from west to east. The distribution trend for the second principal component followed the general decrease in the evaporative potential

TABLE 12. List of climatic variables utilized in principal component analysis (Shaw and Waite, 1964; Shaw, 1981; Decker, 1967; Felch et al., 1972; USDF, 1981)

variable code	variable description
c1	the minimum growing degree units expected to accumulate in 75% of the years during May through October
	-the percentage of years having five day or greater runs of temperature-
c2	above 30 in January 24-30
c3	above 50 in March 22-28
c4	above 50 in October 25-31
c5	above 90 in July 19-25
c6	below 30 in March 22-28
c7	above 50 in January 24-30
c8	the average date of the last freeze in spring
c9	the average first freeze of fall
c10	the average freeze free period in days
c11	the total pan evaporation for April 19 - October 31
c12	the average daily pan evaporation for July 12-18
c13	the mean January temperature
c14	the mean April temperature
c15	the mean July temperature
c16	the mean October temperature
c17	the mean annual temperature
c18	the mean January precipitation
c19	the mean April precipitation
c20	the mean July precipitation
c21	the mean October precipitation
c22	the growing season precipitation mean (April-September)
c23	the mean annual precipitation

TABLE 13. Climatic principal component analysis with variable codes from Table 12 (the first three principal components accounted for 97.6% of total variance based on the correlation matrix)

principal component	eigenvalue
CLIMATE1	20.44
CLIMATE2	2.54
CLIMATE3	0.46

variable code	eigenvectors 1	2	3
c1	.22	-.01	.02
c2	.22	.08	.17
c3	.22	-.07	.14
c4	.22	-.08	.18
c5	.20	.24	-.03
c6	-.19	-.31	.14
c7	-.22	-.03	-.12
c8	-.22	.04	.09
c9	.20	-.17	.07
c10	.22	-.05	-.09
c11	.12	.52 *	-.04
c12	.12	.52 *	-.18
c13	.22	-.03	-.08
c14	.22	-.01	-.12
c15	.22	.03	-.01
c16	.22	.01	-.11
c17	.22	.01	.01
c18	.19	-.24	-.36 *
c19	.20	-.20	.16
c20	-.21	.16	.22
c21	.21	-.13	.01
c22	.18	.14	.74 *
c23	.18	-.32 *	.05

*Major loading factors.

Table 13. (continued)

PREDOMINANT LOADING OF PRINCIPAL COMPONENTS
CLIMATE1 = general climate CLIMATE2 = evaporative environment CLIMATE3 = growing season precipitation

from west to east. The distribution trend for the third principal component followed the general increase in growing season precipitation from west to east.

RESULTS

Introduction

Results in this study have been developed from four data sets. The data sets were the: 1) continuous variables collected in the field and measured in the laboratory describing site factors and species presence, 2) the diameter and age distribution of regenerating species, 3) the compositional patterning and species interactions developed from species associations and crown positions within the stands, and 4) the observations from the field notebooks kept on each sample area. The results section reviews each data set listed above in respective order. Each data set, and each analysis tool or technique utilized, was manipulated to identify the major constraints on oak reproduction occurring in the oak forests of eastern Iowa. Each analysis tool was used separately to identify any constraints suggested by the data. This results section is composed of a number of separate analyses, all attempting to determine oak regenerative constraints.

Conceptual Analysis Development and Preliminary Testing

Regeneration was conceptualized to be controlled by light, soil, water, interference (competition and allelochemics), and climatic factors. From these factors, a detailed working model was developed. The components that comprised this model and that were theorized to be correlated with oak regeneration, were made up of site and species variables. The components of the model were: a) site-energy flux; b) site-water relationships; c) site-soil interactions; d) species interference; e) species-energy relations; and, f) species successional attributes. Table 14 lists the variables that are included in each component group of the model.

Each component group of the model was analyzed separately by linear multiple regression (SAS-STEPWISE by Goodnight, 1982b) to show the relative importance values among component groups over three regeneration types (Table 15). The purpose of this preliminary analysis was for orientation to the data by providing an estimate of which model components were most important and which were least important for white oak, red oak, and total regeneration. Table 15 provides a breakdown of the R-squares of each separate multiple regression and the associated relative ranking of each model component for white oak, red oak, or

TABLE 14. Component variables of the regeneration model

A) Variables of the site-energy flux component.

slope, crown closure, basal area, topographic position, potential radiation input, aspect, general climate, evaporative potential, growing season precipitation.

B) Variables of the site-water component.

slope, litter, topographic position, slope position-moisture, aspect, general climate, evaporative potential, growing season precipitation, clay, pH, phosphorus, magnesium, sand, coarse soil fractions, and nitrogen.

C) Variables of the site-soil component.

slope, litter, aspect, slope-position moisture, topographic position, magnesium, calcium, potassium, nitrogen, clay, sand, pH, phosphorus, coarse soil fractions, and bulk density.

D) Variables of the species interference component.

crown closure, basal area, oak site index, coverage by shrubs, forbs, grass, and unoccupied space, actual number of leaves above the site, and effective leaf area.

E) Variables of the species-energy component.

crown closure, basal area, and actual number of leaves above the site.

F) Variables of the species successional component.

crown closure, basal area, litter, actual number of leaves above the site, and effective leaf area.

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total regeneration. Both white and red oak regeneration were most correlated with site-water relations and site-energy flux variables. White oak regeneration was also correlated with species interference and site-soil interactions while red oak regeneration was correlated more with site-soil variables. The predictive value of the total regeneration multiple regressions are less than the multiple regressions for the oaks. The successional variables, site-energy flux, and site-water relations comprise the top of the R-square values among the total regeneration model components. Because no single model-component-group was strongly correlated to regeneration stocking values, it was decided that all variables from each model component group were to be combined into one large model for subsequent analysis. The variables were not analyzed by separate model component groups, but as a combined set of all variables.

Dependent Variable Definitions

This study attempted to find the correlation of all study variables with oak regeneration. Inherent in the term "oak regeneration" are three regeneration groups, the white oak group, the red oak group, and the white and red oaks as

TABLE 15. Relative importance of component groups based on R-squares for three regeneration groups

component group codes:	
A =	site-energy flux
B =	site-water relations
C =	site-soil interaction
D =	species interference
E =	species-energy relations
F =	species-successional attributes

	regeneration types [1]		
rank	white oak	red oak	total commercial
1.	B (.570) [2]	B (.412)	F (.298)
2.	A (.550)	A (.411)	A (.295)
3.	D (.391)	C (.381)	B (.290)
4.	C (.380)	D (.136)	D (.202)
5.	E (.250)	E (.119)	E (.236)
6.	F (.250)	F (.119)	C (.188)

[1] Defined in Table 16.
[2] R-squared values (probability of a greater F-value is less than or equal to 0.05).

a combined species group. Interfering species were also thought to have an effect on oak regeneration, therefore, other major regeneration groups were included in the analysis for identification of significant associated variables. Finally, the regeneration of any species with sawtimber or veneer value were combined into a single regeneration group and used in the analysis to identify those variables correlated to regenerating commercially valuable tree species. The species regeneration groups utilized in this study and the associated common tree names

that will be used throughout this dissertation are identified in Table 16.

To summarize, the dependent variables in the analysis are the regeneration groups (Table 16). Many of the regeneration groups are composed of several species. For example the white oak regeneration group may contain the regeneration of four different species. For use as dependent variables, each regeneration group or species needed to meet a given minimum level of occurrences within the sample areas to allow for meaningful statistical analysis. Table 17 lists the frequency of occurrence among major regeneration groups and the average regeneration stocking level expected for a sample area on the basis of the data. If a regeneration group or species did not represent 7.0% of the total regeneration and at least 15% average stocking over all sample areas, then that regeneration group or species was not included in the analysis.

The regeneration groups, with their group codes, considered large enough to be included in analysis were sugar maple (SM), white oak (WO), red oak (RO), hickory (HI), ash (AS), cherry (CH), basswood (BS), elm-ironwood (EI), the combined white oak-red oak group (OAKS), and the total commercially valuable regeneration group (TCT).

TABLE 16. List of the regeneration groups, associated codes, and scientific names of trees found on the sample areas (names after Preston, 1976)

regeneration group (code)	scientific name
elm-ironwood (EI)	Ulmus americana L.
	Ulmus rubra Muhl.
	Ostrya virginiana (Mill.) K. Koch
hickory (HI) [1]	Carya cordiformis (Wang.) K. Koch
	Carya laciniosa (Michx.) Loud.
	Carya ovata (Mill.) K. Koch
	Carya tomentosa Nutt.
	Carya glabra (Mill.) Sweet
cherry (CH) [1]	Prunus serotina Ehrh.
	Prunus pennsylvanica L.
	Prunus virginiana L.
red oak (RC) [1]	Quercus rubra L.
	Quercus palustris Muenchh.
	Quercus velutina Lam.
	Quercus ellipsoidalis E. J. Hill
white oak (WO) [1]	Quercus alba L.
	Quercus bicolor Willid.
	Quercus macrocarpa Michx.
	Quercus muehlenbergii Engelm.
ash (AS) [1]	Fraxinus americana L.
	Fraxinus pennsylvanica Marsh.
basswood (BS) [1]	Tilia americana L.
sugar maple (SM) [1]	Acer saccharum Marsh.
	Acer nigrum Michx.
boxelder	Acer negundo L.
black walnut [1]	Juglans nigra L.
butternut [1]	Juglans cinerea L.
hackberry [1]	Celtis occidentalis L.

[1]Species comprising the total commercially valuable species group (red oak, white oak, sugar maple, ash, hickory, cherry, black walnut, basswood, butternut, and hackberry).

Table 16. (continued)

dogwood	Cornus florida L.
quaking aspen	Populus tremuloides Michx.
bigtooth aspen	Populus grandidentata Michx.
cottonwood	Populus deltoides Bartr.
mulberry	Morus rubra L.
honeylocust	Gleditsia triacanthos L.
birch	Betula papyrifera cordifolia (Reg.)Fern.
red cedar	Juniperus virginiana L.
red pine	Pinus resinosa Ait.
hawthorn	Crataegus spp.
juneberry	Amelanchier arborea (Michx.)Fern.
black locust	Robinia pseudoacacia L.
apple	Malus pumila Mill.
	Malus ioensis (Wood)Britt.

Note that the elm and ironwood regeneration were classified as a single regeneration group because of the new role of elm in the forest after Dutch elm disease (Ceratocystis ulmi), and the location of the reproduction of elm and ironwood on the site. The sites where reproduction of each species occurs were observed to be inseparable. Stems of ironwood and elm reproduction occur together on the forest floor forming at times, low canopies of leaves from one to two feet tall. Ironwood seems to eventually outgrow the elms. Elm regeneration continues to be prevalent in most of the understories of eastern Iowa forests. Few of the elms grow larger than sapling size.

TABLE 17. Frequency of occurrence of species over all sample areas and the average stocking percent per sample area

regeneration group	percent of total regeneration	average stocking per sample area (%)
elm [1]	13.1	36.4
hickory [1]	13.0	27.7
cherry [1]	12.0	20.4
red oak [1]	11.0	22.4
ash [1]	10.1	33.3
basswood [1]	9.6	18.3
white oak [1]	7.9	29.3
sugar maple [1]	7.8	49.6
hackberry	3.8	15.0
walnut	2.2	6.1
red cedar	2.2	7.0
boxelder	1.5	9.2
dogwood	1.0	15.7
butternut	0.6	8.5
quaking aspen	0.5	9.8
mulberry	0.5	8.7
ironwood	0.4	9.2
honey locust	0.4	8.2
bigtooth aspen	0.4	3.3
white birch	0.3	26.7
other	1.7	--

[1]Major regeneration groups considered large enough to be included in subsequent analysis.

In summary, from the 30 mil-acre plots on each sample area, a regeneration stocking percent for each regeneration group was developed. The percent stocking of a regeneration group was used as a dependent variable in further analysis.

Independent Variable Definition and Model Analysis

The preparation of the independent variables for analysis accounted for 36 single variables, 12 multiple regression-produced variables (scores) from principal component analysis of soil and nutrient variables with each regression containing 20 variables, and 3 multiple regression-produced variables (scores) from principal components analysis of climatic variables with each regression containing 23 variables. In the whole regeneration model, 51 continuous variables (36 single variables, 15 composite variables) could have been included in the analysis.

Independent variable coding

The continuous independent variables, including the principal component scores for soil, nutrients, and climatic data, used in analysis, are given in Table 18 along with the coding used. Table 19 gives the linear correlations of the independent variables to the regeneration groups. Table 20 summarizes the correlations in Table 19 by listing the five largest correlations for each regeneration group.

TABLE 18. List of the descriptive titles for the independent variable and their associated variable codes

---

X1 = degrees of slope
X2 = transformed aspect azimuth = sin ((aspect - 202.5)/2)
X3 = crown closure at 4.5 feet
X4 = crown closure at ground level
X5 = total basal area of sample area
X6 = basal area of red oak on sample area
X7 = basal area of white oak on sample area
X8 = litter layer depth
X9 = average effective leaf diameter between zero and 4.5 feet
X10 = average effective leaf diameter between 4.5 feet and canopy top
X11 = average effective leaf diameter between zero and canopy top
X12 = crown closure difference (X4 - X3)
X13 = percent of total basal area composed of red oak
X14 = percent of total basal area composed of white oak
X15 = percent of total basal area composed of combined white and red oak
X16 = calculated average effective leaf diameter ((X9 + X10)/2)
X17 = topographic position
X18 = total relative direct and diffuse radiation input possible for the year
X19 = total relative direct and diffuse radiation input possible for the growing season (April-September)
X20 = total relative direct and diffuse radiation input possible for spring warm-up period (Feb. - May)
X21 = total relative direct and diffuse radiation input possible for the maximum photosynthesis period (May-July)
X22 = growing degree units
X23 = oak site index of the sample area
X24 = average site coverage by shrubs
X25 = average site coverage by forbs
X26 = average site coverage by grass
X27 = average unoccupied site coverage

Table 18. (continued)

X28 = average clay content of A horizon
X29 = average sand content of A horizon
X30 = average bulk density of A horizon
X31 = average coarse soil fraction of A horizon
X32 = actual number of leaves over the site between zero and canopy-top = -(log(1-crown closure)/effective leaf area)
X33 = actual number of leaves over the site between 4.5 feet and canopy-top
X34 = effective leaf area over the site between zero and canopy-top
X35 = effective leaf area over the site between 4.5 feet and canopy-top
X36 = soil moisture index of slopes
X37 = CLIMATE1: first principal component score of climatic data (general climate)
X38 = CLIMATE2: second principal component score of climatic data (evaporative environment)
X39 = CLIMATE3: third principal component score of climatic data (growing season precipitation)
X40 = NUTR1: first principal component score of soil data (+Mg = main loading factor)
X41 = NUTR2: second principal component score of soil data (-Ca)
X42 = NUTR3: third principal component score of soil data (-P and -K)
X43 = NUTR4: fourth principal component score of soil data (-clay, +pH, and +P)
X44 = NUTR5: fifth principal component score of soil data (+sand, +coarse soil fractions, and +soil moisture index)
X45 = NUTR6: sixth principal component score of soil data (+pH)

Table 18. (continued)

X46 = NUTR7: seventh principal component score of soil data (-sand and +soil moisture index)
X47 = NUTR8: eigth principal component score of soil data (+soil bulk density, -N, and +P)
X48 = NUTR9: ninth principal component score of soil data (+clay, -coarse soil fractions, and +N)
X49 = NUTR10: tenth principal component score of soil data (+clay and +P)
X50 = NUTR11: eleventh principal component score of soil data (-sand, +soil bulk density, and +N)
X51 = NUTR12: twelfth principal component score of soil data (+clay and -Mg)

Multiple regression analysis

Table 21 lists the multiple regressions produced using the 51 independent variables for each of the regeneration groups. All the regressions found in Table 21 are linear models and were created using SAS (Ray, 1982a,b) software on a NAS-AS/6 (National Advanced Systems, 800 E. Middlefield Rd., Mountain View, CA) mainframe computer. The SAS-STEPWISE (Goodnight, 1982b) routine was used to produce the best stepwise linear "fit" of the data cloud when multiple independent-variables were used. The information listed with the regressions are the whole model R-square value,

TABLE 19. Linear correlations of the dependent and independent variables for regeneration groups (variable codes are from Table 18)

	SM	RO	WO	OAKS	HI	AS
SM	1.000	-0.218	-0.363	-0.320	-0.190	0.160
RC	-0.218	1.000	0.702	0.913	0.306	0.267
WO	-0.363	0.702	1.000	0.932	0.358	0.326
OAKS	-0.320	0.913	0.932	1.000	0.361	0.323
HI	-0.190	0.306	0.358	0.361	1.000	0.364
AS	0.160	0.267	0.326	0.323	0.364	1.000
CH	-0.207	0.027	0.148	0.098	-0.049	-0.047
BS	0.296	-0.143	-0.233	-0.207	-0.052	0.115
BI	-0.263	0.268	0.416	0.376	0.311	0.235
TOT	0.425	0.339	0.300	0.345	0.417	0.556

CH	BS	BI	TOT	X1	X3	X4
-0.207	0.296	-0.263	0.425	-0.079	0.335	0.182
0.027	-0.143	0.268	0.339	0.290	-0.014	-0.014
0.148	-0.233	0.416	0.300	0.164	-0.088	-0.111
0.098	-0.207	0.376	0.345	0.247	-0.058	-0.071
-0.049	-0.052	0.311	0.417	-0.201	0.128	0.112
-0.047	0.115	0.235	0.556	-0.087	0.062	-0.053
1.000	-0.083	0.070	0.209	-0.089	-0.230	-0.183
-0.083	1.000	-0.131	0.277	-0.082	0.094	0.086
0.070	-0.131	1.000	0.104	0.108	0.184	0.202
0.209	0.278	0.104	1.000	-0.112	0.209	0.092

X5	X6	X7	X8	X9	X10	X11
0.349	0.207	-0.201	-0.050	0.274	0.238	0.432
-0.259	-0.101	0.158	-0.056	-0.116	-0.031	-0.137
-0.285	-0.221	0.330	-0.029	-0.304	-0.004	-0.224
-0.295	-0.178	0.270	-0.045	-0.234	-0.019	-0.198
-0.134	-0.195	0.142	0.095	0.136	0.097	0.032
0.079	0.076	0.162	0.046	0.159	0.211	0.226
-0.028	-0.031	0.296	0.078	-0.223	-0.023	-0.194
0.159	0.156	-0.144	0.115	0.360	0.132	0.281
-0.133	-0.098	0.161	0.233	-0.083	-0.029	-0.150
0.114	0.066	0.068	-0.005	0.212	0.359	0.330

Table 19. (continued)

X12	X13	X14	X15	X16	X17	X18
-0.417	-0.304	0.101	-0.220	0.319	0.059	-0.052
0.004	0.248	-0.033	0.219	-0.098	0.069	0.040
-0.031	0.454	-0.175	0.316	-0.206	-0.063	0.179
-0.016	0.387	-0.117	0.293	-0.166	-0.001	0.123
-0.064	0.188	-0.188	0.044	0.139	-0.263	0.191
-0.269	0.151	0.034	0.169	0.221	-0.121	0.092
0.158	0.330	-0.029	0.299	-0.166	-0.075	0.102
-0.039	-0.204	0.112	-0.116	0.321	0.033	0.095
-0.004	0.250	-0.036	0.217	-0.074	0.121	0.193
-0.308	0.087	-0.026	0.065	0.342	-0.066	0.273

X19	X20	X21	X22	X23	X24	X25
-0.037	-0.050	-0.019	-0.375	0.261	-0.524	-0.171
-0.021	0.028	-0.080	0.430	-0.098	0.132	-0.185
0.133	0.169	0.082	0.515	-0.067	0.121	-0.272
0.066	0.111	0.006	0.515	-0.086	0.137	-0.250
0.210	0.195	0.224	0.316	0.082	-0.043	-0.101
0.098	0.092	0.102	0.357	0.094	-0.261	-0.314
0.113	0.104	0.117	0.322	-0.137	0.403	-0.210
0.099	0.097	0.098	-0.369	-0.084	-0.080	-0.158
0.152	0.178	0.116	0.418	0.032	0.069	-0.218
0.266	0.271	0.250	0.255	0.149	-0.225	-0.402

X26	X27	X28	X29	X30	X31	X32
-0.300	0.512	-0.111	-0.239	-0.226	-0.147	-0.165
0.325	-0.198	0.231	0.144	0.431	0.096	0.083
0.564	-0.205	0.164	0.039	0.474	0.087	0.047
0.490	-0.219	0.212	0.096	0.497	0.099	0.069
0.054	-0.049	-0.151	-0.173	0.157	-0.206	-0.009
0.021	0.220	-0.116	-0.140	0.260	-0.171	-0.274
0.241	-0.155	0.070	0.087	0.129	-0.025	-0.028
-0.238	0.317	0.107	-0.015	-0.242	0.035	-0.137
0.269	-0.167	0.181	0.035	0.285	-0.065	0.274
-0.011	0.399	-0.105	-0.122	0.136	-0.118	-0.238

Table 19. (continued)

X33	X34	X35	X36	X2	X37	X38
0.162	0.130	0.320	-0.003	0.075	-0.376	-0.009
0.086	0.001	0.022	-0.143	-0.115	0.464	0.340
-0.062	-0.115	-0.090	-0.136	-0.149	0.552	0.381
0.008	-0.066	-0.041	-0.151	-0.145	0.553	0.391
0.018	0.031	0.083	-0.072	-0.154	0.331	0.103
-0.115	-0.098	0.024	-0.117	-0.051	0.380	0.190
-0.178	-0.208	-0.230	0.093	0.018	0.328	-0.071
0.008	0.088	0.096	-0.058	-0.010	-0.354	-0.115
0.200	0.184	0.175	-0.071	-0.148	0.430	0.230
-0.050	-0.028	0.158	-0.136	-0.148	0.287	0.126

X39	X40	X41	X42	X43	X44	X45
0.527	0.087	-0.035	-0.109	0.284	-0.243	-0.067
0.002	-0.284	0.097	0.161	-0.401	0.167	0.266
-0.018	-0.273	0.131	0.120	-0.438	0.102	0.252
-0.009	-0.302	0.124	0.151	-0.457	0.143	0.280
0.151	-0.445	0.109	-0.071	-0.049	-0.096	0.060
0.415	-0.408	0.116	-0.025	-0.123	-0.082	-0.008
-0.128	-0.079	0.137	0.054	-0.101	0.061	0.046
0.114	0.198	0.093	0.086	0.031	-0.136	-0.018
0.009	-0.194	0.161	-0.090	-0.300	0.095	0.087
0.396	-0.318	0.239	0.125	0.019	-0.173	0.143

X48	X49	X51
-0.026	0.219	-0.009
0.027	0.062	-0.066
-0.047	-0.067	-0.233
-0.013	-0.007	-0.167
-0.020	-0.087	-0.014
-0.064	0.044	-0.125
0.037	-0.226	0.113
0.055	-0.102	0.097
0.064	-0.039	0.045
-0.087	-0.082	-0.026

TABLE 20. List of the five independent variables with the largest absolute linear correlations for each regeneration group

sugar maple		red oak		white oak		oaks	
X39	+0.53	X37	+0.46	X26	+0.56	X37	+0.55
X24	-0.52	X22	+0.43	X37	+0.55	X22	+0.52
X27	+0.51	X43	-0.40	X22	+0.52	X26	+0.49
X11	+0.43	X38	+0.34	X14	+0.45	X43	-0.45
X12	-0.42	X26	+0.33	X43	-.043	X38	+0.39

hickory		ash		cherry		basswood	
X40	-0.45	X39	+0.42	X24	+0.40	X22	-0.37
X37	+0.33	X40	-0.41	X14	+0.33	X9	+0.36
X22	+0.32	X37	+0.38	X37	+0.33	X37	-0.35
X17	-0.26	X22	+0.36	X22	+0.32	X16	+0.32
X21	+0.22	X25	-0.31	X15	+0.30	X27	+0.32

elm-ironwood		total regeneration	
X37	+0.43	X25	-0.40
X22	+0.42	X27	+0.40
X43	-0.30	X39	+0.40
X32	+0.27	X10	+0.36
X26	+0.27	X16	+0.34

which is the amount of variability accounted for by the model, the number of observations included, the mean square error of the model which denotes the amount of variation present, and the standard errors of the individual regression coefficients in parentheses. Unless otherwise noted, the probabilty of a greater F-value occurring is less than or equal to 0.050.

TABLE 21. Multiple regressions of all independent variables for all regeneration groups [1]

---

sugar maple group =
+1.32 intercept
-0.43 (0.15) X24 shrubs
+0.58 (0.13) X27 unoccupied space
-2.36 (0.44) X37 general climate
+17.66 (3.33) X39 growing season precipitation
R-square = 0.560 MSE = 519.33 n=133

red oak group =
+16.91 intercept
+0.76 (0.20) X1 slope
+2.24 (0.33) X37 general climate
+4.27 (0.94) X38 evaporative environment
-46.64 (23.0) X36 SMI
R-square = 0.412 MSE = 294.79 n=133

white oak group =
+19.08 intercept
+0.52 (0.01) X26 grass
+2.02 (0.33) X37 general climate
+5.48 (0.86) X38 evaporative environment
-9.25 (2.64) X51 (+clay -Mg)
+2.01 (0.93) X42 (-P -K)
-3.24 (1.13) X43 (-clay +pH +P)
-61.21 (31.0) X32 actual number of leaves zc
R-square = 0.646 MSE = 230.98 n=133

combined oaks group =
+30.38 intercept
+0.54 (0.18) X26 grass
+3.65 (0.61) X37 general climate
+8.96 (1.54) X38 evaporative environment
+4.71 (1.68) X42 (-P -K)
-6.94 (2.05) X43 (-clay +pH +P)
+5.69 (2.46) X45 (+pH)
-12.40 (4.80) X51 (+clay -Mg)
R-square = 0.614 MSE = 763.6 n=133

---

[1]MSE = mean square error: n = total number of observations: Format order is the regeneration group name, the coefficient for the intercept term, the coefficients and their standard errors for the listed independent variables and descriptive titles.

Table 21. (continued)

---

elm-ironwood group =
-37.95 intercept
+5.75 (1.65) X8 litter depth
+3.83 (1.42) X17 topographic position
+0.06 (0.02) X18 total radiation
+81.77 (37.2) X32 actual number of leaves zc
+2.26 (0.36) X37 general climate
+2.39 (1.04) X38 evaporative environment
R-square = 0.400 MSE = 339.42 n=133

beaswood group =
+113.14 intercept
+7.29 (1.39) X9 leaf diameter zb
-0.04 (0.01) X22 GDD
-0.27 (0.09) X23 SI
-0.30 (0.06) X25 forbs
+1.37 (0.58) X41 (-Ca)
-5.05 (1.58) X49 (+clay +P)
R-square = 0.415 MSE = 134.28 n=133

cherry group =
+2.00 intercept
+0.15 (0.06) X5 BA
+17.14 (5.83) X14 white oak BA
+0.58 (0.09) X24 shrubs
-17.94 (5.34) X34 effective leaf area zc
+18.55 (7.66) X35 effective leaf area bc
+1.65 (0.71) X41 (-Ca)
-4.88 (1.91) X49 (+clay +P)
R-square = 0.422 MSE= 192.56 n= 133

ash group =
+12.02 intercept
+7.42 (2.29) X9 leaf diameter zb
-0.24 (0.12) X24 shrubs
-99.65 (39.4) X32 actual number of leaves zc
+2.54 (0.38) X37 general climate
+3.71 (1.04) X38 evaporative environment
+11.10 (2.74) X39 growing season precipitation
R-square = 0.468 MSE = 348.89 n=133

Table 21. (continued)

```
hickory group =
+38.07  intercept
 -3.41 (1.30) X17 topographic position
 -2.98 (0.56) X40 (+Mg)
R-square = 0.238  MSE = 295.9  n=133


total regeneration group =
+24.92  intercept
-30.89 (10.2) X34 effective leaf area zc
+48.3  (15.8) X33 actual number of leaves bc
 +0.94 (0.40) X37 general climate
 +7.87 (2.37) X39 growing season precipitation
 +1.91 (0.84) X41 (-Ca)
 +1.69 (0.51) X12 crown closure difference
 +0.15 (0.13) X26 grass
 +0.53 (0.13) X27 unoccupied space
 -1.41 (0.63) X40 (+Mg)
R-square = 0.588  MSE = 205.6  n=133
```

Table 21 describes the whole-model regressions for the 10 regeneration groups examined. The most "critical" variable(s) for predicting regeneration of each group are listed and should ideally be viewed "in-whole" as variable groups, not as individual variables. If one variable or site factor was highly correlated to oak regeneration, the possibility is strong that management guides would have utilized this given factor to control regeneration dynamics in the past. Since no one factor is strongly correlated over all sites, a set of variables must be identified and surveyed for their composite effect on oak regeneration. The importance of each individual variable is small compared to the large importance that could occur when the individual variables are brought together in a more complete view of oak regeneration.

Discriminant analysis

Another method used in this study to identify important variables in oak regeneration was discriminant analysis. The software from SAS (Ray, 1982a,b) entitled STEPDISC (Sarle, 1982c) and DISCRIM (Goodnight, 1982a) were used to identify those variables that could discriminate well between two separate regeneration levels.

All continuous variables were inserted into the STEPDISC statistical software to identify, by means of backward elimination, all those variables that were good discriminators between the regeneration states selected. The variables that STEPDISC identified as good discriminators were then inserted into the DISCRIM statistical software to calculate the discriminant function, based upon a pooled covariance matrix, and with rough, un-boot-strapped, misclassification error rates. Table 22 lists the discriminant analysis results for various regeneration states. The information presented with each discriminant analysis is the rough, un-boot-strapped error estimates of site misclassification. The variables listed are the "best" discriminators from the discriminant functions of each regeneration group or level.

To better understand the significance of variables identified by multiple regression and discriminant analysis, all variables found to be constraining regeneration were combined. All the variables from both analysis techniques that were identified as significant in accounting for regeneration stocking values are listed in Table 23. Table 23 allows for the examination of the critical variables and for the potential synthesis of a hypothesis concerning reproduction for a given species.

TABLE 22. Discriminant analysis of regeneration over 14 species/levels to identify critical variables [1]

---

1) Discriminators between all sites and those sites with red oak levels larger than 60% regeneration stocking values (sign is from high red oak sites).

+X32 actual number of leaves zc
-X51 (+clay -Mg)
-X40 (+Mg)
+X1 slope
+X37 general climate
+X24 shrubs

misclassification of high red oak sites = 16%
misclassification of other sites = 8%

2) Discriminators between all sites and sites with white oak levels larger than 60% regeneration stocking values (sign is from high white oak sites).

+X32 actual number of leaves zc
-X51 (+clay -Mg)
+X49 (+clay +P)
+X38 evaporative environment
+X37 general climate
+X26 grass

misclassification of high white oak sites = 8%
misclassification of other sites = 7%

3) Discriminators between all sites and sites with sugar maple levels larger than 60% regeneration stocking values (sign is from high sugar maple sites).

+X39 growing season precipitation
-X37 general climate
+X27 unoccupied space

misclassification of high sugar maple sites = 9%
misclassification of other sites = 22%

---

[1]Format order is the correlated sign of the listed variable and the descriptive variable title with the two associated error rates.

Table 22. (continued)

---

4) Discriminators between all sites and sites with red oak and white oak levels larger than 30% regeneration stocking values (sign is from red oak/white oak sites).

+X36 SMI
+X32 actual number of leaves zc
-X38 evaporative environment
-X37 general climate
+X26 grass
+X1 slope

misclassification of white oak/red oak sites = 15%
misclassification of other sites = 12%

5) Discriminators between all sites and sites with the total commercial regeneration group levels larger than 60% regeneration stocking values (sign is from high total regeneration sites).

+X9 leaf diameter zb
+X41 (-Ca)
-X40 (+Mg)
+X27 unoccupied space
+X26 grass

misclassification of high total regeneration sites = 13%
misclassification of other sites = 18%

Table 22. (continued)

---

6) Discriminators between sites with high sugar maple levels or high red oak levels larger than 55% regeneration stocking values, and corresponding low red oak levels or low sugar maple levels smaller than 45% regeneration stocking values (sign is from high red oak/low sugar maple sites).

+X38 evaporative environment
+X37 general climate
+X17 topographic position
+X12 crown closure difference
+X29 sand content of the A horizon
-X23 SI
+X19 growing season radiation

misclassification of high maple/low red oak sites = 0
misclassification of low maple/high red oak sites = 0

7) Discriminators between sites with high sugar maple levels or high white oak levels larger than 55% regeneration stocking values, and corresponding low white oak levels or low sugar maple levels smaller than 45% regeneration stocking values (sign is from high white oak/low sugar maple sites).

+X37 general climate
+X38 evaporative environment
-X39 growing season precipitation
-X16 average leaf diameter
+X49 (+clay +P)

misclassification of high maple/low white oak sites = 0
misclassification of low maple/high white oak sites = 0

TABLE 23. Variables identified from multiple regression and discriminant analysis as important for the reproduction of several major regeneration groups (correlation sign - variable name)

Good sugar maple sites -
- + growing season radiation
- + growing season precipitation
- + topographic position
- + SI
- + unoccupied space
- + average leaf diameter
- + crown closure difference
- - general climate
- - shrubs
- - clay
- - P

Good red oak sites -
- + general climate
- + evaporative environment
- + slope
- + shrubs
- + actual number of leaves zc
- - SMI
- - clay

Good white oak sites -
- + general climate
- + evaporative environment
- + grass
- + Mg
- - pH
- - K

Good oak sites (combined group) -
- + slope
- + SMI
- + grass
- + actual number of leaves zc
- + Mg
- - P
- - K

Table 23. (continued)

Good total regeneration sites -
+ general climate
+ growing season precipitation
+ grass
+ unoccupied space
+ leaf diameter zb
+ crown closure difference
+ actual number of leaves bc
- effective leaf area zc
- Ca
- Mg

Table 24 lists those variables that are important for maximizing oak reproduction while at the same time, minimizing sugar maple reproduction. Table 24 also highlights those variables that could be most easily manipulated by a forest manager. The most critical factor for oak regeneration that arises from the variable-groups in Table 24 are the requirements for minimizing light interference next to or close to the ground surface. The variables also support the tendency for sugar maple to colonize and control the better sites with the oak relegated to poorer sites.

TABLE 24. Variables identified by multiple regression and discriminant analysis that tend to maximize oak regeneration while minimizing sugar maple regeneration (signs are correlation to max. oak/min. sugar maple)

+	general climate
+	evaporative environment
+	growing season radiation
+	topographic position
+	sand content of A horizon
+	slope
+	pH
+	crown closure difference [1]
+	shrubs [1]
+	grass [1]
+	Mg [1]
-	growing season precipitation
-	SI
-	SMI
-	K
-	unoccupied space [1]
-	average leaf diameter [1]
-	actual number of leaves zc [1]

[1]Variables that could potentially be manipulated.

Analysis of Age and Diameter Data

Introduction

The next set of data analyzed to gain information on the constraints of oak regeneration was from the age and diameter determinations made on forest tree reproduction. For every stem of tree reproduction that occurred, age, diameter, and species were recorded. This stem-by-stem information was recorded on only the four systematically located, intensively surveyed mil-acre plots on each sample area. Some regeneration groups that were found to have large values of reproduction stocking, used as the dependent variable in the preceding analysis, may not have occurred on any of the four more intensively surveyed mil-acre plots due to regeneration distribution patterns. Therefore, not all the major regeneration groups used in site stocking analysis will be present in this analysis.

The important points to remember in this portion of the results section are the differences in the method of sampling, the type of information recorded, and the more limited nature of the age and diameter data, from a statistical point of view, compared with the site stocking values utilized in the preceding analysis.

Graphical examination of age and diameter data

The total number of stems were graphed in relation to all age and diameter data for all the study areas. The generalized distribution of the data has been summarized in Figure 6. The distribution curves of age in relation to the number of stems, and diameter in relation to the number of stems, follows a common exponetial mortality curve. In order to utilize linear analysis techniques, the data were logarithmically transformed. The values of age in years, or diameter in centimeters, were transformed by taking the negative natural log of the inverse of the value. The value for the total number of stems was transformed by taking its natural log. Each regeneration group (Figure 16) was treated separately. The equations of the resultant straight lines that were produced by graphing the transformed data represented the relationship between the transformed number of total stems to the transformed distribution of age or diameter for each regeneration group. The line equations were determined by least squares analysis utilizing SAS-REG (Sall, 1982b) software. Table 25 lists the linear transformed equations of the least squares analysis lines for age in relation to the number of stems. Figure 7 is the graph of the linear transformed equations for age in relation to stem number. The line equations computed for

diameter in relation to the number of stems are given in Table 26. The graph of the line equations for diameter in relation to stem number is given in Figure 8. These graphs and tables review the relationship between the numbers of stems and associated age or diameter measures.

The examination of age versus diameter was also accomplished by using linear analysis techniques (least squares fitting) but with untransformed data (SAS-REG software by Sall (1982b)). The diameter values were put into 1-centimeter-wide diameter classes then the diameter class means were determined. The mean age values for each diameter class were then determined. The diameter class means were graphed in relation to the mean age values. The graphs of the diameter class means in relation to mean age values for the entire sampled population, by regeneration group, are given in Figure 9. The line equations for the diameter class mean in relation to mean age values, by regeneration group, are given in Table 27.

The number of stems in relation to age or diameter analysis can illustrate an interesting parameter. Tables 28 and 29 use the line equation slope values for age and diameter from Tables 25 and 26 to determine the relative velocity of a regeneration group toward extinction on a site. This relative value could also be thought of as an

FIGURE 6. Graphical representation of the general reproduction in relation to age or diameter distribution of the number of stems of

TABLE 25. Line equations for the total number of stems in relation to age by regeneration group (TAGE= -(LOGe(1/age of individual stem)); TSTEMS = LOGe(number of stems))

total regeneration TSTEMS = -2.023 * (TAGE) + 7.55
ash TSTEMS = -2.136 * (TAGE) + 5.99
basswood TSTEMS = -1.625 * (TAGE) + 4.84
cherry TSTEMS = -1.143 * (TAGE) + 4.05
elm TSTEMS = -2.031 * (TAGE) + 6.47
hickory TSTEMS = -1.045 * (TAGE) + 3.80
red oak TSTEMS = -1.585 * (TAGE) + 4.92
sugar maple TSTEMS = -1.400 * (TAGE) + 4.90
white oak TSTEMS = -1.386 * (TAGE) + 4.13

interference tolerance measure over the short-run. The lines, although not all statistically different at the 0.30 level, still provide the best sampled population estimate of data distribution.

Table 30 was derived from viewing the information in Figure 9 during two periods, an initial growth period (1-3 years) and an extended growth period (25-30 years). The initial growth period, on a linear basis, gives a slightly different order of regeneration group growth compared to the extended time period. The graphs in Figure 9, although not fitting the more accurate curvilinear "S" growth function, still suggest the slow initial growth of red oak and the long-term, site dominating, faster growth rates of the oaks in general compared with other species. Again, all the lines are not statistically different at the 0.30 level, but

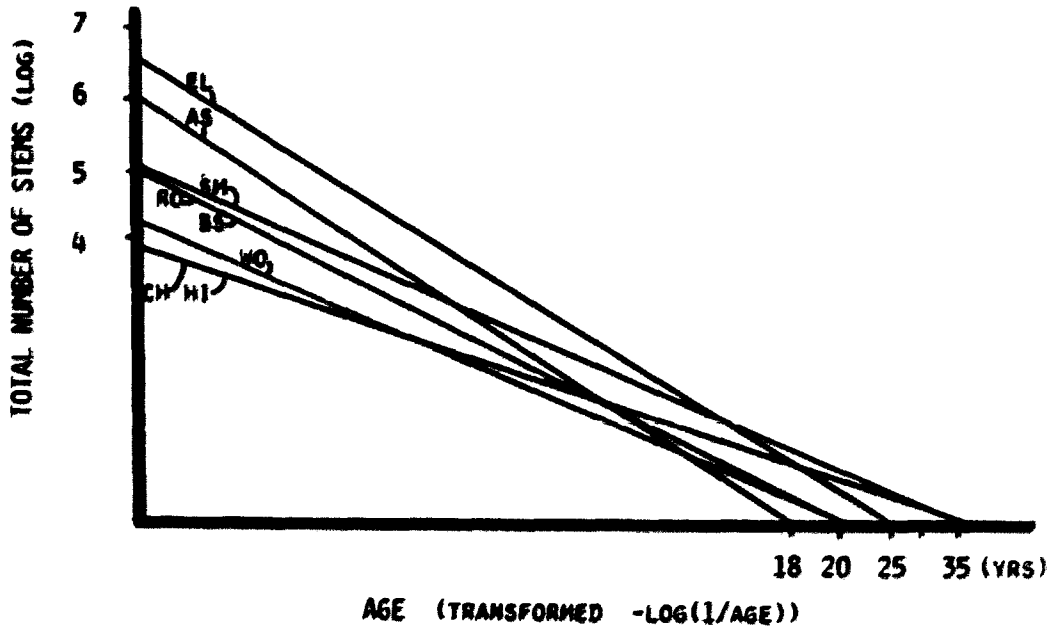


FIGURE 7. Graphs of the line equations for the total number of stems in relation tc age, by regeneration group

TABLE 26. Line equations for the the total number of stems in relation to diameter by regeneration group (TDIAMETER = -(LOGe(1/diameter of individual stem)); TSTEMS = LOGe(number of stems))

total regeneration TSTEMS = -2.931 * (TDIAMETER) + 7.38
ash TSTEMS = -4.272 * (TDIAMETER) + 5.47
basswood TSTEMS = -2.329 * (TDIAMETER) + 4.26
cherry TSTEMS = -3.573 * (TDIAMETER) + 5.06
elm TSTEMS = -2.933 * (TDIAMETER) + 5.68
hickory TSTEMS = -2.178 * (TDIAMETER) + 4.58
red oak TSTEMS = -2.417 * (TDIAMETER) + 4.83
sugar maple TSTEMS = -2.633 * (TDIAMETER) + 5.69
white oak TSTEMS = -2.651 * (TDIAMETER) + 4.84

they still provide the best estimate of the data distribution of the population.

Modification of age and diameter data by integration

The number of stems with a given age or diameter, after logarithmic transformation, produced the graphs in Figures 7 and 8 with the corresponding line equations given in Tables 25 and 26. These graphs and equations present the total sampled population of stems by regeneration group. If the first integral is determined for any of these line equations, the area below the line can be determined. If an intermediate X value is inserted into the first integral of any of these line equations, the area under the line less than or equal to the stated X value can be determined. The

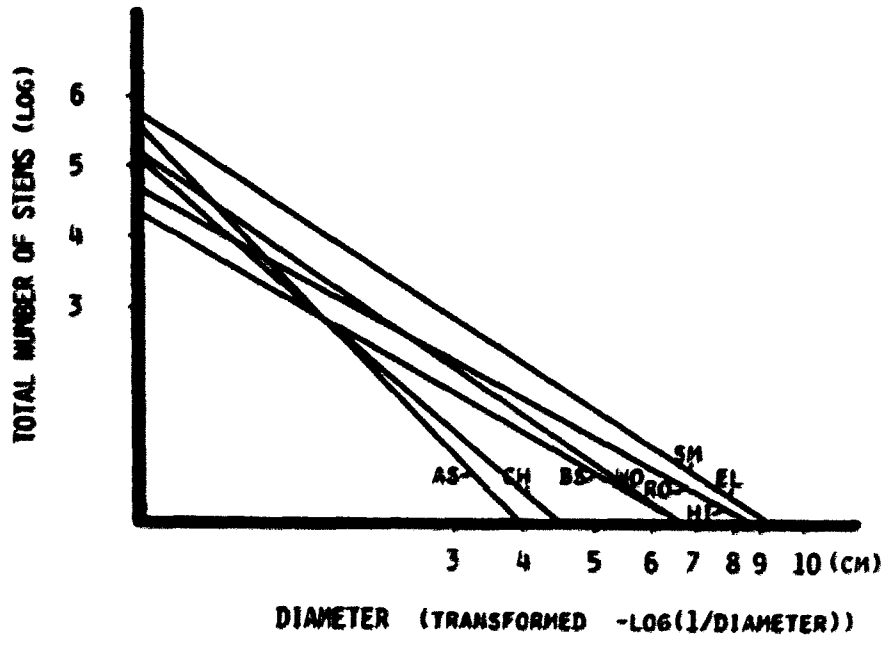


FIGURE 8. Graph of the line equations for the total number of stems in relation to diameter, by regeneration group

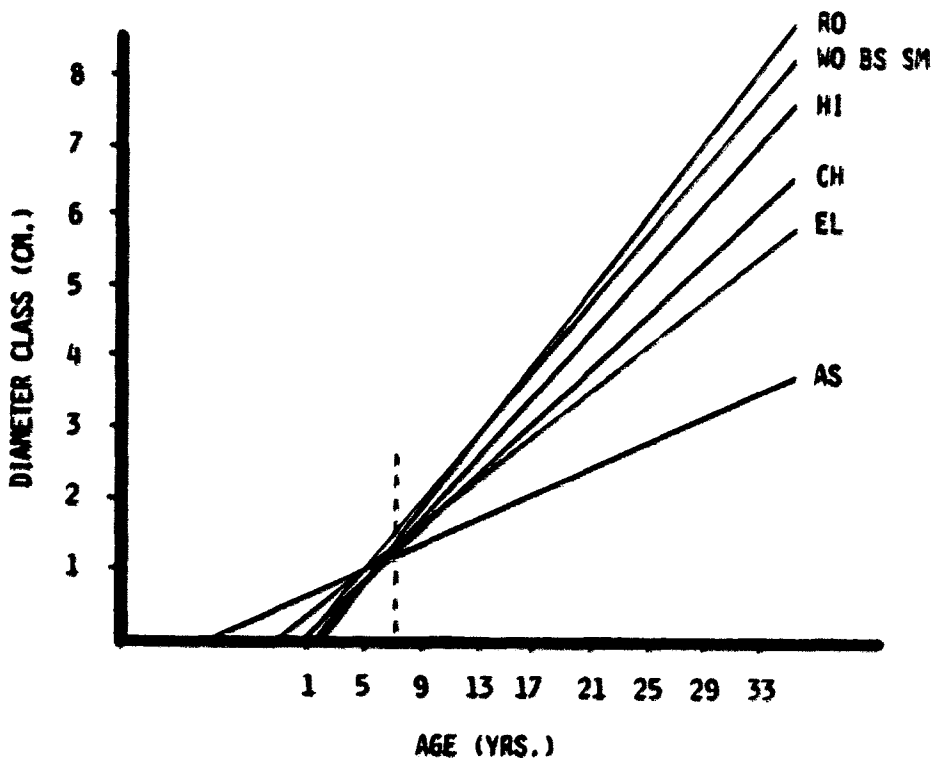


FIGURE 9. Graph of diameter class mean values in relation to mean age values for the entire sampled population, by regeneration group

TABLE 27. Data distribution line equations for diameter class mean in relation tc mean age (DCM = diameter class mean; age = mean age value)

total regeneration DCM = 0.180 * (age) + 0.374
ash DCM = 0.096 * (age) + 0.472
basswood DCM = 0.248 * (age) - 0.366
cherry DCM = 0.194 * (age) - 0.223
elm DCM = 0.155 * (age) + 0.310
hickory DCM = 0.218 * (age) - 0.184
red oak DCM = 0.258 * (age) - 0.427
sugar maple DCM = 0.233 * (age) - 0.136
white oak DCM = 0.240 * (age) - 0.108

TABLE 28. The relative velocity tcward site extinction for each species on the basis cf age, or a general estimate of the short-term interference tolerance (from the slopes in Table 25)

regeneration group	relative extinction velocity
ash	fastest
elm	
basswood	
red oak	
sugar maple	
white oak	
cherry	
hickory	slowest

use of the first integrals of line equations with the logarithmically transformed age, diameter, and numbers of stems values, can allow for the weighting of a given stem in a population by its potential survival within that

TABLE 29. The relative velocity toward site extinction for each species on the basis of diameter, or a general estimate of the short-term interference tolerance (from the slopes in Table 26)

regeneration group	relative extinction velocity
ash	fastest
cherry	
elm	
white oak	
sugar maple	
red oak	
basswood	
hickory	slowest

TABLE 30. Relative rates of diameter growth over time (from Figure 9)

species growth over short-term (1-3 years)	relative position of species	species growth over long-term (25-30 years)
ash	fastest	red oak
elm		white oak
white oak		basswood
basswood		sugar maple
cherry		hickory
sugar maple		cherry
hickory		elm
red oak	slowest	ash

population. Since the landowner is interested in successful regeneration and continued survival, a potential survival weighting system was developed using this integral

technique. This survival weighting system was used to estimate the chances of a stem surviving on a site versus the survival of other stems of that species throughout the study area.

Before each stem was weighted by its potential survival value and the first integral procedure invoked, one population-dependent value called the "critical point" was determined for each regeneration group. The critical points for both diameter and age within each regeneration group, were determined by solving the line equations where the Y value (STEMS) was equal to zero (refer to Tables 25 and 26). For comparison, in untransformed data (Figure 6), the critical point was where the X-axis "tail" of the hyperbola is no longer changing at such a large rate relative to the Y-axis, and is starting to approach the X-axis. In the transformed data (Figures 7 and 8), the critical point is the place where the Y value is equal to zero. The critical point is not a limit, but a place where the sampled population would no longer have a large mortality rate. The significance of the critical point is that beyond it, mortality is relatively low. Critical points calculated for both age and diameter, by regeneration group, are given in Table 31.

TABLE 31. List of the calculated critical points used in the potential survival rating calculations by regeneration group

regeneration group	critical age	critical diameter
ash	16.4 (years)	3.6 (cm.)
basswood	19.7	6.2
cherry	34.5	4.1
elm	24.3	7.0
hickory	38.1	8.2
red oak	22.2	7.4
sugar maple	35.2	8.7
white oak	21.5	6.2
total regeneration	41.7	12.1

When the age or diameter value of an individual stem was less than the respective critical point calculated from the specific regeneration group population, the potential survival of that stem was assumed to be inversely proportional to its distance to the critical point. The larger, or older, the individual stem, the greater the potential survival chances of that stem. The stepwise description of the survival weighting procedure for both age and diameter is composed of two main steps. The first step, (STEP #1), was to determine the total area under the line equation for the entire sampled population of each regeneration group. The first integrals of the line equations from Table 25 for age and Table 26 for diameter were determined and are shown in Tables 32 and 33,

respectively. The specific critical point for age or diameter by regeneration group was then inserted into the integral and the equation solved, producing a value that represents the total area beneath the line equation.

TABLE 32. First integrals of line equations from Table 25 for age values by regeneration group (CRIT=-(LOGe(1/(critical point value for age))); INT = first integral)

ash INT = (((-2.136/2)*(CRIT**2))+(5.99*CRIT))
basswood INT = (((-1.625/2)*(CRIT**2))+(4.84*CRIT))
cherry INT = (((-1.143/2)*(CRIT**2))+(4.05*CRIT))
elm INT = (((-2.031/2)*(CRIT**2))+(6.47*CRIT))
hickory INT = (((-1.045/2)*(CRIT**2))+(3.80*CRIT))
red oak INT = (((-1.585/2)*(CRIT**2))+(4.92*CRIT))
sugar maple INT = (((-1.400/2)*(CRIT**2))+(4.98*CRIT))
white oak INT = (((-1.346/2)*(CRIT**2))+(4.13*CRIT))
total regen. INT = (((-2.023/2)*(CRIT**2))+(7.55*CRIT))

TABLE 33. First integrals of line equations from Table 26 for diameter values by regeneration group (CRIT=-(LOGe(1/(critical point value for diameter))); INT = first integral)

ash INT = (((-4.272/2)*(CRIT**2))+(5.47*CRIT))
basswood INT = (((-2.329/2)*(CRIT**2))+(4.26*CRIT))
cherry INT = (((-3.573/2)*(CRIT**2))+(5.06*CRIT))
elm INT = (((-2.933/2)*(CRIT**2))+(5.68*CRIT))
hickory INT = (((-2.178/2)*(CRIT**2))+(4.58*CRIT))
red oak INT = (((-2.417/2)*(CRIT**2))+(4.83*CRIT))
sugar maple INT = (((-2.633/2)*(CRIT**2))+(5.69*CRIT))
white oak INT = (((-2.651/2)*(CRIT**2))+(4.84*CRIT))
total regen. INT = (((-2.931/2)*(CRIT**2))+(7.38*CRIT))

The second step, (STEP #2), of the procedure was to solve the same integral of the line equation, only this time, insert the specific age or diameter value for an individual stem, as opposed to the critical point value used in the first step (Tables 34 and 35). The values produced by solving these integrals represent the area below the line equations and less than or equal to the specific stem values inserted. If any of the integral values for a specific stem were larger than the integral value for the whole population of a regeneration group, the value of one (1) was used as the survival value for that stem. For all other stems, the survival values were produced by dividing the integral value for a specific stem by the integral value for the entire population of its regeneration group (Step #2/Step #1). The ratio produced was a survival rating value or the probability of a stem surviving to the critical point within its regeneration group.

Refer to Figure 10 for the definitions of survival weighting and analysis terms for the integral procedure. Once a survival value for every stem was determined, the summation of all stem survival values for each sample area, by regeneration group, were used as the dependent variables in multiple regressions. Multiple regressions were used to determine those independent variables from Table 18

TABLE 34. First integrals of line equations from Table 25 of age values for each individual stem (AGE=-(LOGe(1/(age of individual stem))); INTX = first integral of individual X value)

ash INTX = (((-2.136/2)*(AGE**2))+(5.99*AGE))
basswood INTX = (((-1.625/2)*(AGE**2))+(4.84*AGE))
cherry INTX = (((-1.143/2)*(AGE**2))+(4.05*AGE))
elm INTX = (((-2.031/2)*(AGE**2))+(6.47*AGE))
hickory INTX = (((-1.045/2)*(AGE**2))+(3.80*AGE))
red oak INTX = (((-1.585/2)*(AGE**2))+(4.92*AGE))
sugar maple INTX = (((-1.400/2)*(AGE**2))+(4.98*AGE))
white oak INTX = (((-1.386/2)*(AGE**2))+(4.13*AGE))
total regen. INTX = (((-2.023/2)*(AGE**2))+(7.55*AGE))

TABLE 35. First integrals of line equations from Table 26 of diameter values for each individual stem (DIAMT=-(LOGe(1/(diameter of individual stem))); INTX = first integral of individual X value)

ash INTX = (((-4.272/2)*(DIAMT**2))+(5.47*DIAMT))
basswood INTX = (((-2.329/2)*(DIAMT**2))+(4.26*DIAMT))
cherry INTX = (((-3.573/2)*(DIAMT**2))+(5.06*DIAMT))
elm INTX = (((-2.933/2)*(DIAMT**2))+(5.68*DIAMT))
hickory INTX = (((-2.178/2)*(DIAMT**2))+(4.58*DIAMT))
red oak INTX = (((-2.417/2)*(DIAMT**2))+(4.93*DIAMT))
sugar maple INTX = (((-2.633/2)*(DIAMT**2))+(5.69*DIAMT))
white oak INTX = (((-2.651/2)*(DIAMT**2))+(4.84*DIAMT))
total regen. INTX = (((-2.931/2)*(DIAMT**2))+(7.38*DIAMT))

significantly correlated with sample area survival values. The regressions that were developed for the dependent variables of survival-weighted age and survival-weighted diameter are given in Tables 36 and 37, respectively, for

the major regeneration groups. The regressions were produced by stepwise procedures using SAS-STEPWISE (Goodnight, 1982b) software. Note that in these tables, only 7 regeneration groups were included because of the low number of observations found within some of the regeneration groups made statistical analysis unwarrented.

Table 38 summarizes the R-square values from the multiple regressions in Tables 36 and 37. The diameter-based potential survival values tend to have more of their variability accounted for by the regression models than the age-based values. Thus, diameter growth would be a better gauge of continued survival than the age of a stem. This is logical on a carbon incorporation basis and from what is known about sprouting in these upland forests. Table 39 pools those independent variables found in the regression models in Tables 36 and 37 for red oak, white oak, and sugar maple. The variables listed are significant in accounting for potential survival value variability in each regeneration group. The variables suggest that the oaks survive better in the dryer portions of the forest community. Oaks, once established and growing, also survive better if there is a ground cover present below 4.5 feet to minimize interference from other tree reproduction. Litter probably acts to minimize moisture loss.

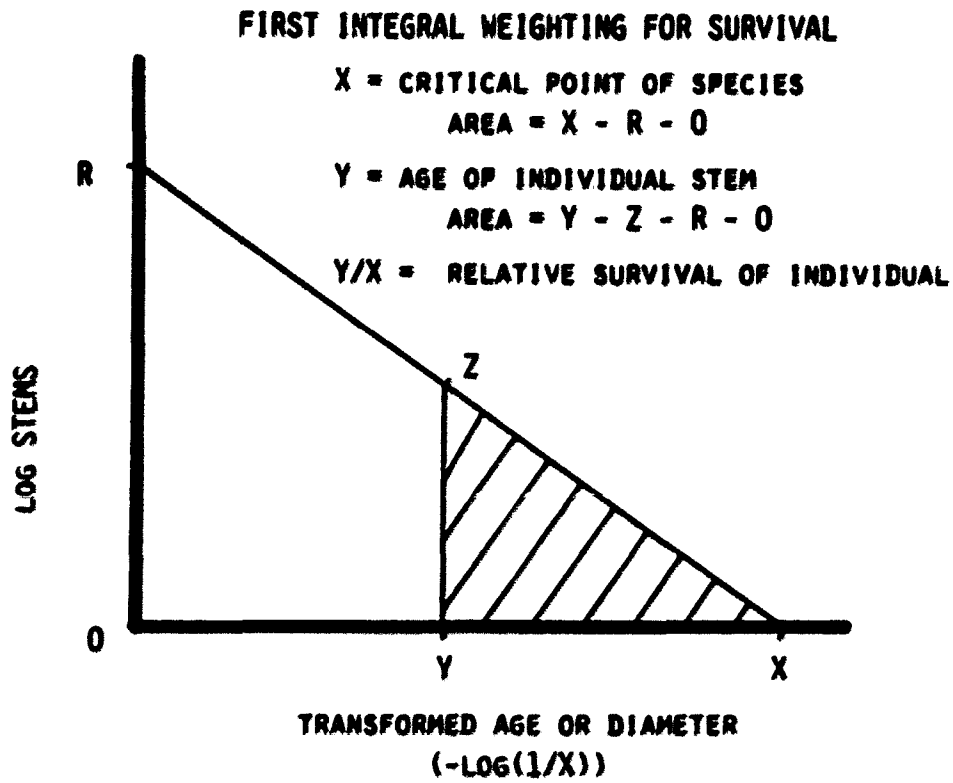


FIGURE 10. Graphical definition of the integral procedure used for weighting each stem by its potential survival

TABLE 36. Multiple regressions of independent variables (Table 18) on the total survival value for a sample area, by regeneration group, on the basis of age data [1]

---

total regeneration group =

-2.42	intercept		
-28.6	(2.90)	X3	crown closure b
+26.1	(3.08)	X4	crown closure g
+2.66	(0.23)	X9	average leaf diameter zb
+4.61	(0.46)	X10	average leaf diameter bc
-5.35	(0.52)	X11	average leaf diameter zc
+0.60	(0.09)	X17	topographic position
-0.04	(0.01)	X25	forbs
+0.07	(0.01)	X26	grass
-1.35	(0.52)	X14	white oak BA%
-67.4	(7.13)	X32	actual number of leaves zc
+146.7	(12.7)	X35	effective leaf area bc
-10.0	(1.75)	X36	SMI
+0.41	(0.07)	X38	evaporative environment
+1.22	(0.17)	X39	growing season precipitation
+0.40	(0.10)	X44	(+sand, +coarse soil fractions, +SMI)
-0.70	(0.16)	X49	(+clay, +P)

R-square = 0.552 MSE = 4.52 N=133

cherry regeneration group =

-0.28	intercept		
+0.19	(0.05)	X1	slope
+1.53	(0.56)	X9	average leaf diameter zb
-0.07	(0.02)	X25	forbs
+0.59	(0.19)	X38	evaporative environment

R-square= 0.455 MSE= 6.12 N=62

---

[1]Probability of a greater F-value is less than or equal to 0.010: MSE = mean square error: N = number of observations: Format order is the regeneration group, the coeffecient of the intercept term, the coeffecient and its standard error for the listed independent variable with descriptive title.

Table 36. (continued)

```
ale-ironwood regeneration group =
 +2.62  intercept
 +1.28 (0.28)   X9   average leaf diameter zb
 -0.05 (0.01)   X25  forbs
 -4.65 (1.27)   X14  white oak BA%
+49.39 (10.7)   X33  actual number of leaves bc
 -1.42 (0.52)   X32  actual number of leaves zc
 +0.29 (0.06)   X37  general climate
 +0.60 (0.14)   X38  growing season precipitation
R-square= 0.506  MSE= 4.13  N=100

hickory regeneration group =
 +5.96  intercept
 +0.67 (0.24)   X17  topographic position
 -0.07 (0.02)   X25  forbs
R-square= 0.200  MSE= 7.37  N=89

red oak regeneration group =
+5.15  intercept
+0.11 (0.05)  X1  slope
R-square= 0.072  MSE= 11.04  N= 77

sugar maple regeneration group =
 +0.61  intercept
 +0.84 (0.23)   X17  topographic position
 +0.15 (0.05)   X28  clay content
R-square= 0.242  MSE= 6.14  N= 90

white oak regeneration group =
 +4.71  intercept
 +1.66 (0.46)   X9   average leaf diameter zb
 -0.14 (0.03)   X25  forbs
R-square= 0.312  MSE= 9.25  N=63
```

Compositional Patterning and Species Interactions

Introduction

"Categorizing forest stands into forest types reduces the usefulness of species composition data and obscures the true pattern of compositional mosaics" (Bell, 1978).

This portion of the results section will attempt to examine and analyze the major interactions between species on a site. The preceding portions of the results section have attempted to analyse the specific species-site interactions. This portion of the results section will view the changing patterns of species composition on the sampled sites both from a vertical, canopy level approach and from a horizontal, species distribution approach. The patterning of compositional changes over time will be addressed and put into a potential management framework. Succession will be considered to be compositional shifts over time based on species-site and species-species interactions with chance playing a large role in the reproductive patterns of a species. The examination of the interactions between the discrete regeneration groups that comprise the forest

TABLE 37. Multiple regressions of independent variables (Table 18) on the survival value for a sample area, by regeneration group, on the basis of diameter data [1]

total commercial regeneration group =			
-72.22	intercept		
-3.21	(0.31)	X9	average leaf diameter zb
+2.21	(0.35)	X11	average leaf diameter zc
+0.20	(0.03)	X12	crown closure difference
+0.02	(0.01)	X22	GDD
+0.03	(0.01)	X24	shrubs
+0.05	(0.01)	X25	forbs
-0.12	(0.02)	X26	grass
+15.6	(3.46)	X34	effective leaf area zc
+20.45	(4.32)	X36	SMI
-6.03	(0.93)	X2	aspect
-1.06	(0.27)	X37	general climate
-0.76	(0.10)	X38	evaporative environment
-2.48	(0.28)	X39	growing season precipitation
-0.47	(0.09)	X41	(-Ca)
+0.72	(0.13)	X43	(-clay, +pH, +P)
-0.88	(0.19)	X48	(+clay, -coarse soil fractions, +N)
+1.41	(0.27)	X51	(+clay, -Mg)
R-square = 0.669		MSE= 9.15	N=133
cherry regeneration group =			
+11.26	intercept		
-5.01	(1.14)	X9	average leaf diameter zt
+0.25	(0.07)	X12	crown closure difference
-0.31	(0.05)	X26	grass
-2.90	(0.64)	X39	growing season precipitation
R-square= 0.624		MSE= 10.72	N=62

[1] Probability of a greater F-value = 0.010: MSE = mean square error: N = number of observations: Format order is the regeneration group, the coefficient of the intercept term, the coeffecient and its standard error for the listed independent variables with descriptive titles.

Table 37. (continued)

```
elm-ironwood regeneration group =
-12.47  intercept
 +1.36 (0.35)  X8   litter depth
 +0.06 (0.02)  X25  forbs
 -0.39 (0.08)  X37  general climate
 -1.08 (0.24)  X38  evaporative environment
 -2.87 (0.58)  X39  growing season precipitation
R-square= 0.558  MSE= 12.39  N=100

hickory regeneration group =
-223.58  intercept
 +10.57 (3.02)  X4   crown closure g
  +0.07 (0.02)  X22  GDD
  +0.13 (0.03)  X24  shrubs
  -3.24 (0.85)  X37  general climate
  -1.67 (0.26)  X38  evaporative environment
  -2.61 (0.60)  X39  growing season precipitation
  +0.87 (0.30)  X43  (-clay, +pH, +P)
R-square= 0.598  MSE= 10.83  N=89

red oak regeneration group =
-10.71  intercept
 +0.22 (0.08)  X12  crown closure difference
 -0.41 (0.10)  X37  general climate
 -3.04 (0.85)  X39  growing season precipitation
R-square= 0.460  MSE=19.94  N=77

sugar maple regeneration group =
 -6.84  intercept
 +0.28 (0.07)  X12  crown closure difference
 -0.11 (0.04)  X26  grass
 -0.22 (0.06)  X28  clay content
R-square= 0.337  MSE= 9.88  N=90

white oak regeneration group =
-14.87  intercept
 -0.08 (0.03)  X7   white oak BA
 +3.45 (0.68)  X8   litter layer depth
 -5.06 (1.00)  X39  growing season precipitation
R-square= 0.510  MSE= 21.12  N= 63
```

TABLE 38. Comparison of the age and diameter based multiple regression R-squares for the survival rating values from Tables 36 and 37

regeneration group	age R-squares	diameter R-squares
total regeneration	0.552	0.669
cherry	0.455	0.624
elm-ironwood	0.506	0.558
hickory	0.200	0.594
red oak	0.072	0.460
sugar maple	0.242	0.337
white oak	0.312	0.510

TABLE 39. The independent variables from Table 18 that were found to be statistically significant in accounting for the survival rating variability of red oak, white oak, and sugar maple

red oak group-
- \+ X1 slope
- \+ X12 crown closure difference
- \- X37 general climate
- \- X39 growing season precipitation

white oak group-
- \+ X9 average leaf diameter zb
- \+ X8 litter layer depth
- \- X25 forbs
- \- X7 white oak BA
- \- X39 growing season precipitation

sugar maple group-
- \+ X17 topographic position
- \+ X12 crown closure difference
- \- X26 grass

should, at least, allow the species-site interactions identified in the preceding analysis to be put into the context of a whole forest community. This portion of the results section will move past the tree to examine the forest. It should be noted that these data were taken only on sites with oak reproduction present, and therefore, do not completly address all upland forests in eastern Iowa.

Regeneration and succession are inherently wedded. Succession on a given site is the differential establishment and growth, hence resource utilization, by an assortment of species that have had their propagules transported to that site. One tree, or group of trees, because of internal biological constraints, external architecture, and/or eventual death, can not continue to control all the resources over an entire site. The existence of reproduction can be thought of as a measure of resource availability on a given site. The interference for available resources is great and death is, by far, the most likely result of tree seed germination. The continual survivors of interference are "heir-apparent" to the top canopy positions on a site. If the reproduction present is of the same species as the overstory trees, then little net compositional change will be observed. If the reproduction present is a different species than the overstory, time and

genetic-environmental interactions will determine how great, and to what extent, species composition will change on a site. The foundation assumption for this portion of the results section is that the reproduction currently on a site will be the next dominant forest canopy upon removal or death of the current canopy. This is an assumption allowed by oak-hickory forest types. Violations of this assumption will partially destroy the functionality of the observations developed from species interactions in this portion of the results section.

General data summary

The first step taken in examining species-species interactions was to summarize what was present on the sampled sites. The data were gathered from the regeneration stocking values on each sample area, from the individual stems occupying the four, intensively surveyed mil-acre plots, and from the identification of the canopy species over those four mil-acre plots in order of their relative vertical position in the canopy. Table 40 provides an accounting, on an individual mil-acre basis, of the percent of all mil-acres stocked by a major regeneration group. Table 41 lists the dominant regeneration found on the sample areas divided into three general groupings. Table 42 lists

the predominant crown types identified over all sample areas. These tables are a general summary of the data.

TABLE 40. The occurrence of major regeneration groups in the understories of upland forests in eastern Iowa on an individual mil-acre basis with 90% of all mil-acres being occupied

rank	regeneration group	percentage of total
1	elm-ironwood	18.5
2	sugar maple	15.0
3	hickory	13.6
4	ash	13.0
5	red oak	9.5
6	cherry	9.0
7	white oak	8.9
8	basswood	6.6
9	other varied species	5.9

TABLE 41. Major regeneration groups in the understories of upland forests in eastern Iowa on a sample area basis

group	percentage of total
sugar maple	40.9
white oak - red oak	44.5
white oak - sugar maple - red oak	7.8

TABLE 42. Dominant crown types of the upland forests of eastern Iowa over all sample areas

species group	percentage of total
white oak	29.5
red oak	25.0
sugar maple	11.3
hickory	7.5
elm	7.5
basswood	3.2
walnut	2.9
ash	2.3
cherry	2.2

Analytical categories of regeneration and crown types

To simplify the observations of regeneration group stocking values on each sample area, cluster analysis was used to divide the sample areas into specific regeneration classes or types. The statistical similarity between the regeneration on different sample areas were calculated, then allocated into discrete classes. The separate classes of regeneration can be treated as distinct forms of species-species and species-site interactions. Within a given regeneration class, the interference and site attributes impinging the genetic material available can be assumed to be more similar than the site and species characteristics leading to the regeneration of another class, recognizing that chance regeneration probabilities exist.

The clustering analysis and regeneration class allocation were completed by SAS-CLUSTER (Sarle, 1982a) and SAS-TREE (Howell and Sarle, 1982) software using Ward's minimum variance method (Johnson and Wichern, 1982). Ten classes of regeneration were developed from this analysis and are listed in Table 43 with the percent of all sample areas found to be in each class.

TABLE 43. Regeneration classes developed from cluster analysis

code	regeneration classes	percentage of total
1	cherry - basswood	15.8
2	oak - hickory - cherry	5.3
3	oak - hickory	11.3
4	oak	6.8
5	oak - hickory - ash	10.5
6	oak - sugar maple - hickory - ash - cherry	9.0
7	sugar maple - ash - cherry	4.5
8	sugar maple - hickory - ash - basswood	22.6
9	sugar maple - cherry - ash	7.5
10	sugar maple - oak - ash - basswood	6.8

The next step in categorizing the species interations on the sample areas was the identification of the general overstory types found to give rise to each regeneration class. The breakdown of crown types for each regeneration class was distinct and produced 4 crown types leading to the

10 regeneration classes. Table 44 lists the four crown types identified and the percent of the sample areas with each type of crown coverage.

TABLE 44. The four general overstory types found associated with the ten regeneration classes developed from cluster analysis

type code	species group	percentage of total
A	oak	18.1
B	oak - hickory	31.6
C	oak - ash	13.5
D	sugar maple - oak	36.8

The ten regeneration classes and the four crown types, in combination, account for every compositional permutation encountered. Table 45 lists the crown types with the associated regeneration classes (all by code symbols) that can arise beneath these crown types. The variance of the different regeneration classes occurring below a given crown type signifies the differential dispersal, establishment, and survival abilities of different species interacting with site attributes, all governed by chance occurrences and changing success probabilities.

TABLE 45. All the observed combinations of the four crown types and the ten regeneration classes (codes from Tables 43 and 44)

crown type codes	associated regeneration class codes
A	1, 2, 4
B	2, 3, 6
C	5, 7
D	8, 9, 10

Successional trends

A question that arose was that if the lack of oak regeneration and/or the proliferation of maple in the understory of oak stands was a part of a natural ebb and flow of compositional shifts inherent in the present stand, what are the future compositional shifts to be expected? The successional trends within the forests of eastern Iowa need to be understood in the context of compositional shifts and resource availability for intelligent management. The expected compositional shifts in the stands were estimated by the development of a successional flow diagram.

The successional flow diagram was produced by first examining the dominant overstory on each site and characterizing the overstory by the primary canopy and by the secondary canopy, if present. Figure 11 illustrates the definitions used for the two canopy layers. The dominant

overstory was determined by examining the vertical distribution of the canopy, by species, above the four intensively surveyed mil-acre plots on each sample area. Each of these mil-acre plots usually had a given species in both the primary and secondary canopy. Comparing the canopy list of species from the four mil-acre plots on each sample area allowed for the determination of a dominant primary and secondary canopy for the site. In most cases, the four overstory samples available gave an accurate estimate of the dominant canopy because at least three of the four mil-acres had the same overstory. In the sample areas where the primary or secondary canopies were not readily apparent from the sample data, the sample area overstories were determined from the field notebook descriptions of the site. The field notebook descriptions were also used to check the accuracy of using the four mil-acre sample procedure for canopy determinations. The sampling procedure was found to accurately identify the dominant overstory of a sample area 85% of the time.

The regeneration occurring on each site was determined from the site stocking values. When the regeneration stocking values were used directly from the data set, little successional information was gleaned because of the preponderance of the ash, hickory, cherry, and elm-ironwood

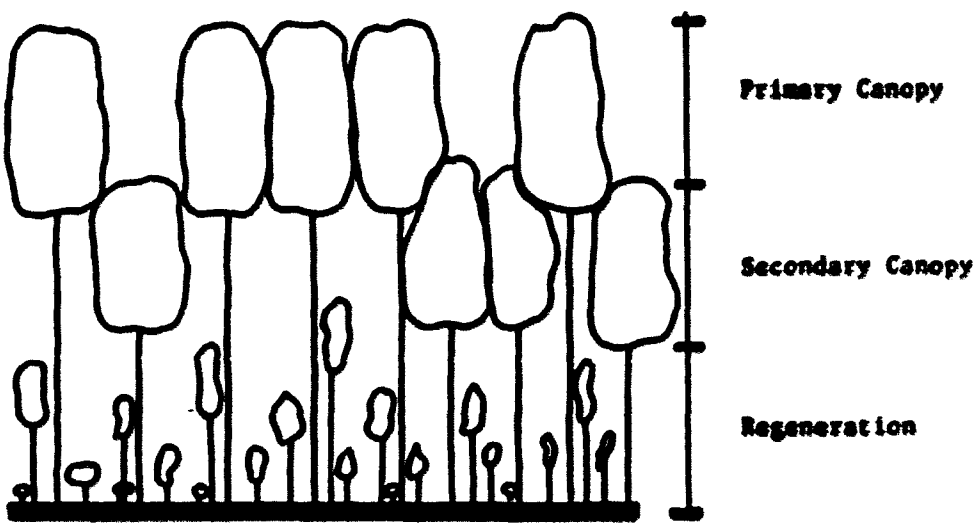


FIGURE 11. Diagram of the definitions used for the canopy layers

regeneration groups. If sheer numbers of stems determine ultimate success on a site, the forests of eastern Iowa would be dominated by a hickory-cherry forest with ash pockets. Assuming that major regeneration changes have not occurred over the past 50 years, the oaks and sugar maple, despite their relatively low number of stems of reproduction per site, are continuing to dominate the forest. Also, the pole-size stems found in the forests are rarely ash, hickory, or cherry. Ash, hickory, and cherry reproduction are experiencing a high rate of mortality while the stems of oak and maple continue to survive. It became apparent that to eliminate the compositional "noise" produced by the large numbers of stems that had high mortality rates, a relative importance value, or survival weighting factor, for each regeneration group was needed.

The regeneration stocking values were multiplied by an importance weighting factor that resulted in a stocking value that more accurately simulated the relative survival value of one regeneration group versus another regeneration group. The estimates of survival differences, used in the importance weighting factors, were derived from a ratio of the number of overstory trees (ecological successes) to number of stems of regeneration (potential ecological successes) over all sample areas, by regeneration group.

The assumptions are that; 1) this ratio has been roughly the same in the near-past and will remain so into the future, and 2) that an area-wide survival ratio will be equivalent to a specific, small-area survival ratio. Both of these assumptions are somewhat tenuous but, the ratio of mature canopy trees to stems of reproduction does provide an estimate of the differential survival rates and future stand value for stems of reproduction in eastern Iowa that is producable without extended research and permanent regeneration plots with individual stem marking.

The relative survival ratios were called "regeneration importance numbers" and are listed in Table 86. The regeneration importance number (RIN) for each regeneration group, multiplied by the regeneration stocking of each regeneration group on the site, yields a species dominance number (SDN) for each regeneration group. Therefore, the stocking percentage for each regeneration group on a site multiplied by the regeneration importance number produces an estimate of the ability of each species to control the site. For example, the potential future success of one stem of white oak reproduction is roughly equivalent to eleven stems of cherry reproduction. The summation of all the SDN for each regeneration group on a sample area produced the regeneration dominance value (RD). The RD value provided a

relative level of site dominance by all the reproduction on the site.

TABLE 46. Regeneration importance numbers based on crown occupants to regeneration ratios within a regeneration group

regeneration group	regeneration importance number
white oak	3.3
red oak	2.6
sugar maple	2.5
hickory	1.2
basswood	1.2
ash	0.3
cherry	0.3
all other species	0.0

The results of these mathematical manipulations with regeneration stocking values were an idealized present regeneration status, a "most likely" compositional change vector (SDM values), and a potential velocity of future compositional change (RD values). These determinations located the forested site successionally, by knowing the overstory and reproduction present, and provides a probabilistic direction for future compositional shifts. Stands may seem to be at similar stations successionally, but are actually in the process of differential change. Identification and classification of the dominant overstory

alone, or in combination with non-tree-reproduction understory species, might not recognize the differential composition changes occurring, and therefore, be meaningless over the rotation age of the stand in accounting for productivity from tree crops and for tree reproduction changes that could eventually dominate the site. This successional classification system will help to correct these inherent problems.

In this study, it was conceptualized that for proper management of oak-hickory forests, only those crop-species predominantly involved with new site colonization, and continual survival and growth in the understories, were critically important to identifying potential compositional change. There was a large amount of reproductive "noise" present in the forests of eastern Iowa and some form of selective filter was required to understand the dominant compositional change vectors. The weighting of regeneration by regeneration importance numbers was the selective filter used. RIN weighting rewards past reproductive success and assumes that the same level of success will continue.

A frequency analysis of all overstory species/ regeneration groups revealed a jumble of different compositional combinations differing in the amount of reproduction from each regeneration group occurring beneath

the various canopy combinations. But, if each regeneration stocking value was multiplied by the regeneration importance number for that species, the less important species were functionally eliminated. The less important species may reproductively triumph on a microsite or a set of microsites by chance or by inhibition of other species' reproduction, but will have little effect on the compositional complexion of the forest. This weighting system is concerned with area-wide occurrences, not individual cells of reproduction. Hackberry (Celtis occendentalis) capturing and holding one microsite is inconsequential in the forest dominated by reproducing oak and maple. The reproductive successes that this weighting system is attempting to highlight are the most probable occurrences.

A separate compositional group was produced from those species with small regeneration importance numbers and called "other species". The "other species" class (code = ZZ) does account for a sizable number of regeneration groups. This does not imply that all regeneration groups respond in the same manner within the understory, but simply that on an area basis, each minor regeneration group was not critically important to the management of the stand due to its isolation or being a non-crop species. One notable exception was black walnut (Juglans nigra) where one

isolated stem may signify more potential monetary value than a usual stand. In this study, walnut did not occur often enough to evaluate its interaction with other species and to the site, so it was included with the other species.

Another consequence of having the "other-species" class was the error rates produced. Any site will be taken over by those species that first successfully regenerates the site. The "other-species" regeneration group members may dominate a given site for decades but, over many stands and time, the major regeneration groups will continue to predominate most of the forested areas. Regeneration management is for an area of forest, not individual spots on the forest floor. Strong regeneration stocking of a species over an area will provide general dominance of the site. A few areas of the understory will continue to be held by "other species". Monoculture on a site, the dominance by one species, is a stressed condition in a natural community and interference tends to force species diversity to increase. Forecasting regeneration success and dominance for the major regeneration groups will always be prone to error. Including the "other species" regeneration group will increase the accuracy of the forecast but significant errors will still occur.

The primary and secondary canopies, and the regeneration type, after weighting with the RIN, were identified for each sample area and a frequency distribution produced. For each sample area, an overstory type was identified (Tables 47), and a regeneration type (Tables 48). Also, a regeneration dominance value for each sample area was produced by summing all the species dominance numbers (SDN) for a sample area.

TABLE 47. Crown types, codes, and sample percentages for sampled areas of eastern Iowa forests (coding example: AABB = AA is primary crown: BB is secondary crown)

crown types (primary-secondary code)	percentage of total
red oak - sugar maple (ROSM)	14
other species - other species (ZZZ)	14
sugar maple (SM0)	14
white oak (WOO)	12
white oak - red oak (WO-RO)	9
white oak - elm - ironwood (WOEI)	9
red oak (ROO)	8
white oak - sugar maple (WOSM)	6
hickory (HIO)	5
other species - sugar maple (ZZSM)	3
white oak - hickory (WOHI)	3
red oak - elm - ironwood (ROEI)	3

By using importance-weighted regeneration values and by eliminating the variance of other species by the inclusion

TABLE 48. Major regeneration classes identified, after weighting with RIN, on a sample area basis

regeneration types	percentage of total
sugar maple	29
white oak - red oak	27
white oak	11
sugar maple - red oak	10
white oak - sugar maple - red oak	8
red oak	7
white oak - sugar maple	2
other	6
cherry - basswood	(1)
basswood	(2)
hickory	(1)
cherry	(1)
ash	(1)

of an "other species" group, a pattern of compositional shifts was realized (Figure 12). The flow rate values between the groups or cells in Figure 12 are the relative number of sample areas moving in a given direction. Assuming a systematic sampling technique, with adequate number of data points, for a specific area of eastern Iowa, the successional flow diagram in Figure 12 will act as an estimate of compositional change occurring in the oak regenerating, upland forests. The figure was derived from the compositional flow vectors from all sample areas contined in a frequency analysis. For example, if the canopy type was red oak and the regeneration type was white

oak-red oak and there were 11 sample areas moving away from red oak toward white oak-red oak then the rate of change listed would be 8 (11/133). It should be remembered that the flow diagram represents a general pattern of flow for sites having oak reproduction present, and therefore, does not encompass all forested sites in eastern Iowa.

Table 49 lists the dominant compositional flow vectors used to produce the successional flow diagram (Figure 12). A point of interest is that sugar maple and the white oak - red oak groups are the only groups reproducing themselves. All other groups are moving toward either the sugar maple or the white oak - red oak groups. The pivotal flow-diagram cell is in the center where compositional shifts produce a combination oak - maple group. As can be seen in Figure 12, natural shifts will favor flow toward sugar maple.

Markovian analysis of the successional flow diagram

To better understand the consequences of the flow pattern produced, a Markov chaining program (after Horn, 1971) was developed and used to better understand internal flow patterns (Figure 13). The basic software used to develop the program was SAS-MATRIX (Sall, 1982a). The results of using Markov chaining techniques are given in Table 50. Table 50 provides a glimpse of where the internal

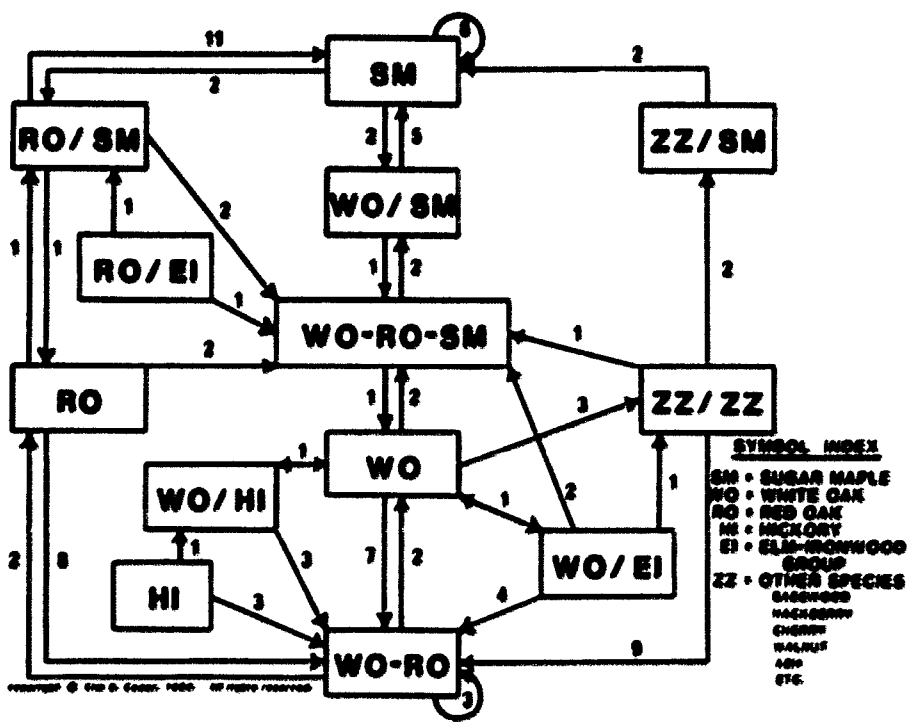


FIGURE 12. Successional flow diagram for upland forests in eastern Iowa

TABLE 49. Compositional change vectors in the forest stands of eastern Iowa

red oak - sugar maple TO sugar maple
other species - other species TO white oak - red oak
sugar maple TO AND FROM sugar maple
white oak TO white oak - red oak
white oak TO other species - other species
white oak - red oak TO AND FROM white oak - red oak
white oak - elm - ironwood TO white oak - red oak
red oak TO white oak - red oak
white oak - sugar maple TO sugar maple
hickory TO white oak - red oak
other species - sugar maple TO sugar maple
white oak - hickory TO white oak - red oak
red oak - elm - ironwood TO white oak - red oak
red oak - elm - ironwood TO sugar maple - red oak
red oak - elm - ironwood TO white oak - maple - red oak

compositional flow is going and suggests what could be done to "short-circuit" natural compositional shifts in favor of maintaining oak. Note that the initial flow (short-term dominance) is toward oak stands, but that eventual "leakage" toward sugar maple is present.

The value of the Markovian analysis technique is that it can show where the predominant flows or shifts are occurring over various time-frames. From the Markovian analysis, two interesting points arose. The first point is, because of the nature of a Markov chain, a stationary species composition is reached after a number of iterations. This characteristic is a function of the analysis tool, not

number of iterations	forest state matrix [1]		regeneration matrix [2]		new forest state matrix [3]
step 1	MATRIX A	*	MATRIX S	=	MATRIX B
step 2	MATRIX B	*	MATRIX S	=	MATRIX C
.	.		.		.
.	.		.		.
.	.		.		.
step n	MATRIX N	*	MATRIX S	=	MATRIX N [4]

[1] From field or artificial data (1x10 array).
[2] Successional flow diagram (10x10 array).
[3] (1x10 array).
[4] MATRIX N is the copposition steady-state ("climax").

FIGURE 13. Functional description of the Markov chaining technique utilized in the analysis assuming 10 regeneration groups are incorporated

TABLE 50. Identifying the major flow patterns within the compositional flow diagram using Markov chain analysis

forest state percentages	short-term dominance	long-term dominance	number of iteration cycles
actual field values	36% WO-RC 29% SM 11% WO-SM-RO	46% SM 15% WC-RC 11% WC/SM	19
100% WC-SM-RO	67% WO/SM 33% WO	same as above	11
50% RO - 50% WO	62% WO-RC 16% WO-SM-RO	same as above	27
100% WC	42% WO-RO 29% RO 29% WO	same as above	30

necessarily the forest stand studied. The "climax" or the stationary state reached at the end of Markov chaining must be the same for any starting state value since the regeneration matrix (i.e., the flow diagram) will always be the same. The climax forest produced is an artificial attribute of the analytical tool but does suggest where the longterm flows are going.

The final state reached, using actual field data as input, was one dominated by sugar maple with the oaks still present in the stands (Table 50). The intermediate compositional shifts show an initial movement toward oak-

dominated stands with a slow flow toward the final dominant, sugar maple. The initial gross flow is toward the oak end of the flow diagram while the longterm net flow continues to go toward sugar maple. If the longterm flow toward sugar maple could be slowed or short-circuited, oak dominance could be maintained or even increased on the study sites.

The second point of interest in the Markovian analysis is the number of iterations required to reach the inevitable stationary end point (Table 50). Since the number of iterations can be thought of as an internal clock mechanism, the relative number of iterations needed to reach the final state can suggest the presence of flow-disruption or flow-slowing due to specific changes in the initial starting percentages. In this analysis, the presence of sugar maple pushes the compositional flow toward compositional steady-state (with sugar maple as the dominate) relatively quickly. With sugar maple excluded from the stand at the beginning, the composition pattern does not reach a common end point for a much longer period of time. This pattern suggests that continual pressure on the sugar maple would keep the compositional pattern away from equilibrium indefinitely, creating a managed quasi-stationary position where the oaks would remain as the stand dominants.

Regeneration dominance classes

Another stand attribute that arose from successional trend analysis was the potential use of regeneration dominance values and associated classes. Regeneration dominance values are the summation of all the species dominance numbers (SDN) on a sample area, and estimates the level of site dominance by tree reproduction. Table 51 shows the regeneration dominance classes developed in this study. The larger the regeneration dominance class number (regeneration dominance value), the faster the compositional-change rate toward site domination and therefore, successful stand colonization and predominance of a species. The regeneration dominance class is an estimate of the velocity with which the composition in the stand is changing. Coupled with information on the overstory and regeneration type, each sampled area could be classified by where, compositionally, the area is now, where the area is going, and an expectation of how quickly the area will get there. A site can be classified by this technique and, when mapped, could provide a regeneration management guide.

Determining species-species and species-site interactions

Interactions between species can suggest which species is undergoing the majority of compositional change and which

TABLE 51. The regeneration dominance classes developed in this study and the percent of the sample areas in each class

regeneration dominance class	regeneration dominance value	descriptive term	percent of total sample areas
1	0 - 25.0	changeable	14.4
2	25.0 - 60.0	marginal	24.5
3	60.0 -	dominance	61.2

species is responsible for compositional change pressure. One method used for identifying species-species interactions was by comparing the linear correlations of all regeneration groups with each other using the regeneration stocking values. The correlations suggest complementary, antagonistic, or neutral relationships between regeneration groups. Table 52 lists the linear correlations for the major regeneration groups.

If each regeneration group is taken separately, and the linear correlations of the other regeneration groups to it are viewed, the interactions between regeneration groups can be examined. To more clearly visualize the relationships involved, Table 53 lists those regeneration groups negatively correlated with each regeneration group. Table 53 can be thought of as listing, for each regeneration group, of the largest associated interfering regeneration groups.

TABLE 52. Linear correlations of regeneration groups for regeneration groups (SM=sugar maple, RO=red oak, WO=white oak, HI=hickory, AS=ash, CH=cherry, BS=basswood, and EI=elm-ironwood)

	SM	RO	WO	HI	AS	CH	BS	EI
SM	1.00	-0.22	-0.36	-0.19	0.16	-0.21	0.30	-0.26
RO	-0.22	1.00	0.70	0.31	0.27	0.03	-0.14	0.27
WO	-0.36	0.70	1.00	0.36	0.33	0.15	-0.23	0.42
HI	-0.19	0.31	0.36	1.00	0.36	-0.05	-0.05	0.31
AS	0.16	0.27	0.33	0.36	1.00	-0.05	0.12	0.24
CH	-0.21	0.03	0.15	-0.05	-0.05	1.00	-0.08	0.07
BS	0.30	-0.14	-0.23	-0.05	0.12	-0.08	1.00	-0.13
EI	-0.26	0.27	0.42	0.31	0.24	0.07	-0.13	1.00

Table 53 presents the major interference "contests" occurring in the understories of eastern Iowa forests. The sugar maple-basswood regeneration groups and the oak-hickory regeneration groups are challenging each other for establishment sites and resources. An interesting relationship can be found between ash and cherry, in that both regeneration groups, traditionally held to be gap colonizers, interfere with each other but, it is clear that ideal cherry sites are not equivalent to ideal ash sites. Table 53 suggests that cherry interferes on the more moist understory sites with hickory, sugar maple, and basswood. Another relationship of interest is the interference between the sugar maple-basswood regeneration groups and the elm-ironwood regeneration group. From this data, the elm-

TABLE 53. Regeneration groups found to have negative linear correlations with each regeneration group

regeneration group	interferers
sugar maple	white oak elm-ironwood red oak cherry hickory
basswood	white oak red oak elm-ironwood cherry hickory
red oak	sugar maple basswood
white oak	sugar maple basswood
elm-ironwood	sugar maple basswood
hickory	sugar maple basswood cherry
cherry	sugar maple basswood hickory ash
ash	cherry

ironwood regeneration group responds similarly with the drier-site upland regeneration groups to sugar maple-basswood interference.

Another method used for examining species-species interactions was to use the regeneration group stocking values from each sample area with backward stepping, stepwise multiple regression techniques. The dependent variable was the stocking of one regeneration group and the independent variables were the stocking of all the other regeneration groups. This procedure determines the regeneration group found to be significantly positively and negatively related to every other regeneration group. The sign of the regression coefficients and the significant independent variables (regeneration groups) identified, denote general interactions between the regeneration groups.

The multiple regressions were produced using SAS-STEPWISE (Goodnight, 1982b) software and are given in Table 54. The intercept term, the coefficients and their standard errors, the significant variables identified, and the model R-square, mean square of the error, and the number of observations are listed for each regression.

The first obvious point to take away from Table 54 is the regeneration groups that are negatively related to each single regeneration group. The major area of interference

TABLE 54. Multiple regressions of regeneration groups on individual regeneration groups (probability of a greater F-value is less than or equal to 0.05)

---

elm-ironwood group =
 28.1 intercept
  0.34 (0.08) white oak
  0.22 (0.10) hickory
R-square = 0.220 MSE = 439.9 n = 133

basswood group =
  3.67 intercept
  0.09 (0.04) sugar maple
 -0.12 (0.06) white oak
  0.10 (0.05) ash
R-square = 0.138 MSE = 191.5 n = 133

cherry group =
 21.5 intercept
 -0.11 (0.04) sugar maple
R-square = 0.048 MSE = 289.1 n = 133

ash group =
 -0.51 intercept
  0.24 (0.06) sugar maple
  0.38 (0.08) white oak
  0.34 (0.10) hickory
  0.24 (0.13) basswood
R-square = 0.290 MSE = 455.2 n = 133

hickory group =
 16.3 intercept
 -0.10 (0.05) sugar maple
  0.14 (0.08) red oak
  0.23 (0.07) ash
  0.14 (0.07) elm-ironwood
R-square = 0.237 MSE = 324.9 n = 133

white oak group =
  0.29 intercept
 -0.17 (0.04) sugar maple
  0.62 (0.07) red oak
  0.18 (0.06) ash
  0.16 (0.06) elm-ironwood
R-square = 0.608 MSE = 247.7 n = 133

Table 54. (continued)

red oak group =		
7.47	intercept	
0.64 (0.05)	white oak	
R-square = 0.503	MSE = 246.7	n = 133
sugar maple group =		
38.7	intercept	
-0.41 (0.12)	white oak	
-0.24 (0.14)	hickory	
0.44 (0.11)	ash	
-0.24 (0.14)	cherry	
0.37 (0.17)	basswood	
-0.20 (0.12)	elm-ironwood	
R-square = 0.315	MSE = 808.9	n = 133

is between the sugar maple regeneration group and the white oak-hickory regeneration groups. The cherry and elm-ironwood regeneration groups are also interfering with the sugar maple regeneration group, and the white oak regeneration group is interfering with the basswood regeneration group. These relationships, governed by the limitations of the technique, especially with the low R-square values, still suggest the main interactions that are occurring in eastern Iowa forests.

The second point that arises from Table 54 is the y-intercept term for each model. The y-intercept terms from all the regeneration groups suggest the capacity for one regeneration group to tolerate interference from other

regeneration groups and the site in general. Table 55 lists the y-intercept terms from the multiple regression models in Table 54 in relative order of their interference tolerance.

TABLE 55. Y-intercept terms from Table 54 listed in order of interference tolerance (1 = most interference tolerant)

rank	regeneration group	intercept term
1	sugar maple	38.7
2	elm-ironwood	24.1
3	cherry	21.5
4	hickory	16.3
5	basswood	9.7
6	red oak	7.5
7	white oak	0.3
8	ash	-0.5

A third point that can be gleaned from Table 54 is the complementary patterning from the positively related regeneration groups. If all the regeneration groups with positive regression coefficients signs are examined, complementary groupings can occur that may suggest species reinforcement (pseudo-facilitation) factors and/or similar site requirements. From this information, several composite forest regeneration types can be identified: 1) sugar maple - basswood regeneration groups; 2) oak - hickory - elm - ironwood regeneration groups; and, 3) ash - cherry

regeneration groups. The ash-cherry regeneration groups survive as some portion of both of the first two groups, and although ash and cherry do not have the same interference tolerance, they do reproduce, survive, and grow following similar ecological-physiological strategies (i.e., gap-phase).

With the relative ranking of interference tolerance from Table 55, the regeneration group relationships from Table 53 can be modified to show those regeneration groups most critical in interference. Table 56 lists the major interference interactions between regeneration groups corrected for their interference tolerance. Table 56 was created by taking the information in Table 53, then eliminating any regeneration group as a major interferer that has a lower interference tolerance level (from Table 55) than the regeneration group in question.

Table 56 lists the important interactions between regeneration groups, as opposed to general interactions. A regeneration group that can strongly interfere has a greater probability of surviving and of controlling growth (resource uptake) than a regeneration group that may only interfere weakly. While Table 53 listed all the interactions identified by linear correlations, Table 56 lists only those interactions with the largest portion of potential interference.

TABLE 56. The major interference interactions between regeneration groups corrected for relative interference tolerance (derived from Tables 53 and 55)

regeneration group	major interference interactions
sugar maple	---
basswood	elm-ironwood cherry hickory
red oak	sugar maple basswood
white oak	sugar maple basswood
elm-ironwood	sugar maple
hickory	sugar maple cherry
cherry	sugar maple
ash	cherry

If the major interference interactions listed in Table 56 and the relative interference tolerance positions were the only rules governing compositional change and eventual dominance in a forest, successional patterns could be summarized for these sites as shown in Figure 14.

The final analytical technique that was used for examining species-species interactions was to take the regeneration group stocking values for each sample area and

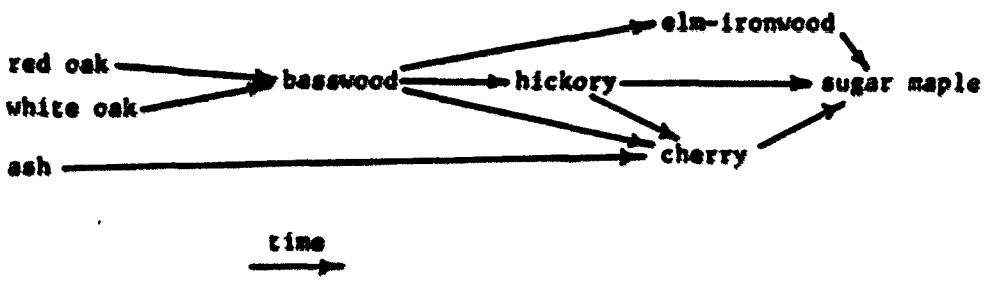


FIGURE 14. Successional pattern development produced from regeneration group interactions and the relative interference tolerance values for each regeneration group

use principal component analysis to determine regeneration group distribution along the principal axes of data distribution. Considering the regeneration stocking data set as a cloud of data points, the predominant orthogonal axes along which the points are distributed can be identified. Regeneration groups that interfere with each other a great deal and are found under different species-site conditions will be the dominant loading factors within different principal components. By examination of the dominant loading factors in the principal components, estimates of species interactions can be made.

The software utilized was SAS-PRINCOMP (Sarle, 1982b). The eigenvalues and eigenvectors developed from the correlation matrix are listed in Table 57. The dominant loading factors are marked.

Examining the dominant loading factors of the principal components suggests specific interactions between regeneration groups and shows which regeneration types are responding similarly, or differently, relative to each other. The first principal component (PC1) differentiates between the traditional upland, drier-site regeneration groups and the moister site, understory elm-ironwood group. The second principal component (PC2) defines an axis in the data cloud where sugar maple, basswood, and ash occur. Ash

TABLE 57. List of the eigenvalues and eigenvectors from the correlation matrix of regeneration stocking values on regeneration stocking values

principal component	eigenvalue
1	2.83
2	1.94
3	1.07
4	0.84
5	0.73
6	0.68
7	0.51
8	0.25

	eigenvectors							
	1	2	3	4	5	6	7	8
SH	-.16	+.57 *	-.02	-.25	-.30	+.30	+.37 *	-.10
RO	+.45 *	-.08	-.05	-.53 *	+.32	+.02	+.17	+.60 *
WO	+.49 *	-.18	+.03	-.27	+.18	+.10	-.06	-.76 *
HI	+.39 *	+.07	-.23	+.37 *	-.20	-.67 *	+.26	+.01
AS	+.36 *	+.35 *	-.12	+.08	-.23	+.16	-.78 *	+.16
CH	+.10	-.12	+.92 *	+.16	-.10	-.03	-.03	+.12
BS	-.09	+.46 *	+.06	+.31	+.81 *	-.04	-.08	-.05
BI	-.34 *	-.17	-.13	+.56 *	-.01	+.65 *	+.31	+.11

*Dominant loading factors.

occurs in both PC1 and PC2 suggesting a non-specific site preference, as long as a gap (sufficient light) is present. PC3 suggests the unique role of cherry in the stands of eastern Iowa. Cherry varies along a distribution axis of its own, probably involving its massive dispersion sphere, low establishment rates, large seedling mortality rates, and

forest edge or gap site requirements. PC4 is an axis that differentiates between red oak and hickory-elm-ironwood regeneration groups. PC5 is the basswood axis. PC6 differentiates between hickory and elm-ironwood. PC7 differentiates between ash and sugar maple. PC8 differentiates between red oak and white oak.

The first three principal components, responsible for 67% of the variation in the data, show the interactions between major regeneration groups or types while the remaining principal components divide the data along single regeneration group axes. The first three principal components define the "role" regeneration groups play within the forest. The significance of these findings can be summed up into three items. The first item is that ash would seem to take regeneration sites away from both the oak-hickory regeneration groups and the sugar maple-basswood regeneration groups. The second item is that elm-ironwood interfers with the oak-hickory regeneration groups much more than with the sugar maple-basswood regeneration groups. The third and final item is that cherry operates as an anomaly within the regeneration patterns of eastern Iowa, probably due to specific site requirements.

Interference levels

Table 58 was developed from examining the interactions (interference) between canopy occupants and the regeneration beneath those occupants for a sample area, as determined from the four intensively sampled mil-acre plots. Table 58 gives relative intraspecific interference values determined from a regeneration group regenerating beneath its own species. The lower the ratio the less tolerant the species is to its own interference. Sugar maple is the most tolerant of regenerating beneath its own species while ash is least tolerant. The resource interfered with the most is probably photosynthetically active radiation (PAR).

Table 58 also gives relative interspecific interference values determined from a regeneration group reproducing beneath another species. The larger the value, the more reproduction found beneath another species. The interspecific interference values are more representative of the shear numbers of individuals present on the sample area and of the variablility of the microsite, both of which probably greatly outweigh the interference effects. All species listed have a small specific interspecific interference effect on reproduction beneath them while differences in microsite and general resource preemption effects from all species have a much greater affect on the reproduction present.

TABLE 58. Relative intraspecific and interspecific interference values determined from a regeneration group regenerating beneath its own species or a regeneration group reproducing beneath another species

species	intraspecific [1] interference value	interspecific [2] interference value
sugar maple	19	2.2
white oak	16	1.3
red oak	8	1.7
elm	7	2.5
hickory	5	1.9
basswood	3	1.0
cherry	3	1.4
ash	1	2.0

[1]The lower the ratio the less tolerant the species is to its own interference.
[2]The larger the value, the more reproduction found beneath another species.

The same effect is not found in the intraspecific values, as suggested by the high relative value differences between the highest and lowest intraspecific interference values with the expected maximization of reproductive capacity near the mature tree. The lack of the expected reproduction increase near the mature tree, especially in the case of basswood, cherry, and ash suggest that other factors are at work interfering with successful regeneration. Allelochemics or intensive competition for non-light resources, regardless of traditional light

tolerance and crown density factors, would seem to control reproduction in these species.

The final measure of species-site interaction utilized was to approximate the relative "size" of the regenerating microsite and/or estimate the interactions between the microsite and the intraspecific interference tolerance of a regeneration group. The resultant value was estimated from the average number of stems of reproduction for a given regeneration group expected on the mil-acre plots of the sample area that contain at least one stem. In other words, the mil-acres where there are no stems of a regeneration group are eliminated and only those mil-acres with at least one stem of reproduction are counted. The result is a "packing density" value where if a mil-acre is stocked with a regeneration group, the estimated number of stems to be found on that mil-acre are given in Table 59 For example, the sugar maple regeneration group should average 2.9 stems per mil-acre if found at all.

The significance of these values are that they can estimate the number of stems present in the field from a stocking occurrence measure on mil-acre plots, and provide a relative level of intraspecific interference tolerance between regeneration groups. The larger the value the more intraspecific interference tolerant a regeneration group

TABLE 59. The average number of stems of a given regeneration group occurring on a mil-acre plot if the plot has at least one stem of the same regeneration group present

regeneration group	packing density values
sugar maple	2.9
basswood	2.0
white oak	1.7
elm-ironwood	1.7
hickory	1.6
ash	1.5
red oak	1.5
cherry	1.4

should be. The sugar maple regeneration group is the most tolerant (2.9), while the cherry regeneration group is the least tolerant (1.4).

Field Notebook Information

The final portion of the results section is information recorded for each plot in the field notebooks. This information was gathered from field observations that are not easily quantifiable but was of forest or stand-wide importance. Overstory species, understory species, past-use, and present-use were a portion of the recorded information. Also, successional trends were recorded on the

plots so composite information over all the sample areas might be produced. The field notebooks contain information about individual plots as well as observed generalities on the forest stands pertinent to survival, growth, and regeneration. The notebooks are biased by the education and experiences of the observer but, can provide a overview of the areas sampled and may provide a source of hypotheses for potential experimentation. The information reviewed here is from observations made over several sites and recorded multiple times in the field notebooks.

Grazing

Approximately 60% of the plots examined were being grazed or had been grazed in the past. Grazed sites seemed to have fewer plant species represented but, a greater grass and woody-shrub component, and were more compacted and/or eroded. One of the immediate problems to be aware of was the variation in the definition of grazing intensity between landowners and foresters, and among landowners. For example, in conversations with land owners concerning past, present, and future use of the sampled areas, the level of grazing was discussed. My definition of light grazing is the use of forest understories for the feeding of domestic livestock where the total forest resource is visually

effected little and should continue growth and regeneration at only slightly reduced rates. The definitions of the landowners for light grazing ranged from my definition to a parkland type area with heavy sod and scattered trees. Another "lightly grazed" site was bare of an understory and the overstory trees were being damaged by compaction and physical damage of stem tissues. Again, these examples are from plots where there was only "light" grazing by the definition of the landowner.

Sites that never had been grazed lacked woody ground cover and the understories were more open. Heavily grazed sites had large woody-brush components in the understory, no tree regeneration, and poor residual stand growth. The shrub understory seemed to predominate on the site, eliminating effective regeneration for 25 - 30 years before break-up of the shrub canopy would occur, assuming grazing was discontinued. On plots where the precise years of grazing were known, even light to moderate grazing produced significant losses of growth increment and the distruction of most reproduction.

Grazing acts as an ultimate inhibition stress responsible for mature trees reaching life-end with no chance of replacement. The forest, under heavy grazing, exists as a stressed overstory until the premature death of

the canopy trees leaves a shrub layer behind as the site dominator. The forest "evaporates" away from the bottom up. An example can be seen on a prairie-forest edge. If reproduction of the trees is allowed by the environment, the trees will invade the prairie. Alternately, if regeneration is not allowed, as the current edge trees die, the forest edge is pushed back and the prairie invades the forest. It should be clear from knowing the dispersal and growth patterns of prairie and forest species that the balance of the forest edge can be shifted in favor of the prairie species with only occasional destruction of forest regeneration.

On the sample areas observed, a hierarchy of animal users developed that showed potential abuse of the forest resource. From the worst grazing animal to have in a forest to the "best", the list follows; buffalo, cattle, horses, sheep, and swine. Of course, the intensity of use is not a function of the animal as much as the attitudes and experiences of the landowner, but swine grazing seemed to have less of an adverse effect on the upland oak forests than cattle. The method of grazing and animal food selection also interact with intensity to determine the effect on resource use. Grazing does tend to select for thorny species and species that sprout profusely. Also,

elimination of grazing increases growth rates at most grazing intensity levels and from any animal-user group.

For the oaks, it was critical to have the reproduction above the predation line of the grazing animal. With average growth values, oak should be susceptible to direct grazing of photosynthetically active material for 7 - 10 years. From stands having many different grazing regimes, one method for attempting to regenerate oak could be to heavily graze a site one year then eliminate grazing for 7 - 10 years. A modified method would be to graze at moderate intensities for 2 -3 years then stop grazing for 7 - 10 years. Control of the shurb component will be needed to maximize the probability of tree regeneration. Grazing removed in the late summer before heavy mesting might lead to higher probabilities of successfully regenerating masting trees such as the oak.

High-grading

High-grading was another noticeable problem with Iowa forest stands. Approximately 50% of the sites sampled were significantly high-graded. Only 20% of the sites sampled had ever been harvested with regard to proper regeneration. Thirty percent of all plots were so badly high-graded that attempted correction of the problem is beyond normal

cultural practices of thinning and general timber stand improvement. These badly abused sites would probably take the equivilent of 3-5 rotations to recover phenotypically if good genotypes were available for colonization.

Badly abused sites will require clearance of stems with subsequent planting to approach a reasonably productive level similar to other local stands. High-grade cutting is still continuing by single tree selection by the landowner, and by a failure of loggers and contractual agreements to recognize the ecological necessity of crop tree harvest with trash tree reduction.

Fuelwood development

Much of the forest stands away from the major river-stream areas are in steep waterways and inholdings among crop land. The volume present in these scattered pockets of woodland seem to be great. Proper management, considering landowner objectives, could potentially yield large amounts of firewood and some sawtimber. Most of this woodland area is currently not used or abused by inappropriate grazing and dumping of farm residues and trash. On a small farm, productive woodland inholdings could produce some measure of value not being realized presently. The presence of individual stem damage on many sites suggest fuelwood as a viable, continuously producing, alternative.

Crown architecture

The concept of crown position and dominance was found not to be applicable to eastern Iowa forests in the traditional sense. A "dominant" crown position is a sign of canopy changes in the stand and a strong probability of stem mortality. Horn's work (Horn, 1971) on crown type relations works well in the study forests but not specifically for the reasons surmised by Horn. A dominant crown position or emergent, in most cases, is under some form of canopy stress that forces long shoot growth to occur. The dominant tree is forced away from the stress by outgrowing the codominants. Codominants form a more or less continuous layer that causes self-pruning in the dominant and codominants. Also, since dominants can be a less light-tolerant species, the codominant canopy layer, usually composed of more light-tolerant species, removes more and more photosynthetic area over time from the crown of the dominant stem.

The interaction of the dominants and codominants is comparable to several candles burning in a basin with water slowly rising around them. The candles represent the dominants and the water represents the codominant canopy

layer growing with time. The dominants are slowly snuffed out. This mechanism is seen in eastern Iowa in oak-maple stands. The crowns of oak are pushed up into dominant positions by the codominant sugar maples. As the crowns of oak are forced upward to maintain electron balance, the trees become visibly more prone to pest attack, have less live crown and therefore, less flowering and fruiting. The final result is that regeneration around dominants declines with time to become almost non-existent. The terms that should be used in describing functional crown positions are:

traditional term	functional term suggested
dominant	escapists
codominants	dominants
intermediate	sub-dominant
suppressed	suppressed

Another architectural observation also arising from Horn's work is live crown thicknesses. In the forest, if crowns are viewed as a verticle cross-section relative to the forest floor, the verticle thicknesses of the crowns vary from tree to tree. The reason for this undulation in crown thicknesses arises from the species present and their relative light tolerances. Low-light tolerant species tend to have mono-layered photosynthetic arrays. Low-light

intolerant species have multi-layer photosynthetic arrays. In cross section, crowns of shade tolerant species have thin crowns and shade intolerant species have thick crowns. In the forest, "waves" of differential crown thicknesses are present. The wave is thickest near gaps and escapists trees and thinnest in the dominant trees. The thickness of the wave is dependent upon PAR extinction, the species strategy for capture of the PAR, and the ability of a species to properly maintain function and growth. In eastern Iowa the sugar maple, which is usually in the codominant position with a mono-layered photosynthetic array stresses oaks into escapists or dominant crown positions. The oaks attempt to maintain multi-layered crowns by long-shoot growth, but eventually form a mono-layered crown which will lead to death. Contrary to the suggestions in the literature, species do interconvert crown growth patterns over time in response to stress and resource availability.

The stereotypic oak wolf-tree could never exist in a sugar maple dominated forest. Oak undergoes dramatic phenotypic changes in response to crown crowding from the side or below. The crowns are not wide-spread and may appear to be more excurrent under crown stress. The branches are generally smaller in diameter and have a sharper branch angle. As the 15% live crown ratio is

reached, death becomes an almost inescapable result for oak. Crown ratio would seem to be a good predictor of potential mortality and a "meter" of how well cultural treatments have worked. The oak wolf-trees were developed under almost no light resource stress.

Compositional patterning

From the successional flow diagrams produced over the sampled sites, a composite diagram was produced and is given in Figure 15. The flow diagram shows the major pathways that sites have followed in the past, apparent from age group structure on the sites, and from present compositional changes. The interesting point to note is the interrelation between species groups and the lack of a clearly defined pathway. The traditional facilitation model of succession is probably not accurate in the forest system of eastern Iowa.

Most of the forest stands occurred on slopes surrounding streams and rivers. The general composition of the stands are shown in Figure 16. This figure is a composite of many slopes and stands and so, does not exist itself. The important points of Figure 16 are: 1) that oak is dominant on the slope just below the top of the hill down to sidslope and, 2) that sugar maple dominates from midslope

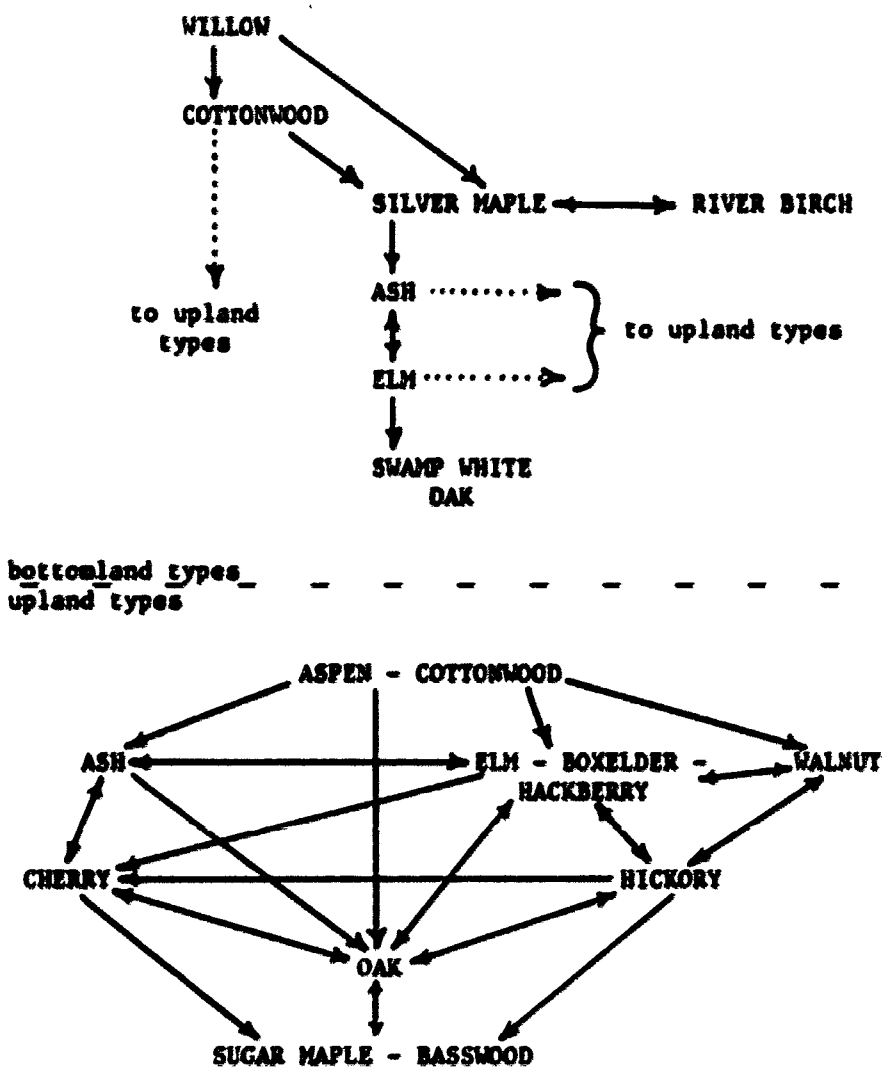


FIGURE 15. Composite successional flow diagram produced from observations over many sample areas

down almost to the bottom. Again this is a general compositional trend. There exists sugar maple stands on the tops and oak stands in the bottom but, due apparently to moisture availability, the basswood-maple association is found on the more moist lower half of the slope and in cove areas while oaks dominate where there are more periodic moisture shortages as on the top of the slopes.

In the field notebooks, there are many notes concerning the role of a species in the forest. A list of some of the more common observations are given in Table 60.

Most species can regenerate beneath any other species. The chances for regeneration occurring may be less but, regeneration can still occur regardless of the traditional view of the successional position of a species. On a given microsite, there must exist a probability that determines regeneration success on each site. Even if the probability is small that cottonwood, for example, will regenerate beneath oak, the probability still exists and cottonwood can be found regenerating beneath oak. Species that are most expected to regenerate, or more precisely, those species with the highest probability of regenerating can be managed. Unexpected failures in regenerating crop species will always occur and is a function of the small probabilities associated with regenerating other species. Success in

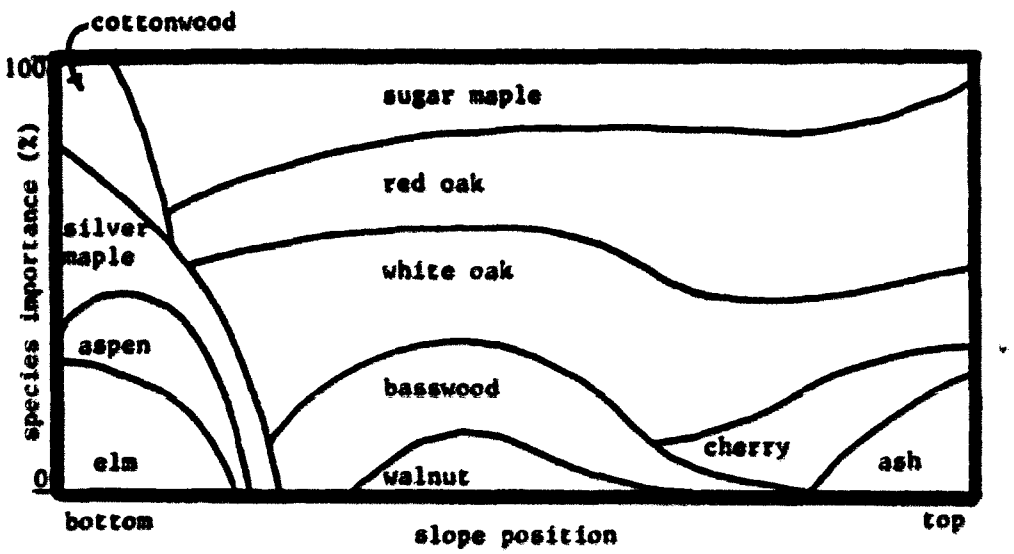


FIGURE 16. Composite diagram of forest composition over many slopes

TABLE 60. Sample regeneration events of one species reproducting beneath another species

oak beneath hickory
oak beneath elm
oak beneath cherry
oak beneath birch
oak beneath sugar maple
hickory beneath oak
elm beneath oak
cherry beneath oak
birch beneath oak
sugar maple beneath oak
cottonwood beneath oak

regenerating a particular species will depend on the site characteristics and the probability of regenerating that species relative to the probabilities of regenerating the other species in the area whose dispersal spheres overlap the site.

For example, oak could be underplanted in a cathedral stand of sugar maple with little maple regeneration and little understory, as is common in old maple stands, and be expected to survive, grow, and move into gaps left by crown damaged maple. Crown thinning would increase the chances of oak gaining the overstory if interference is eliminated at the ground level. Planting oak under maple where it would not ordinary have a high probability of germinating and growing, would bypass some of the critical points in the

regeneration cycle of oak in a maple stand. Planting increases regeneration probabilities immensely.

Successional Climax

To know where each stand is located on the successional continuum of all the sampled sites, the terminal successional state needs to be defined to act as a limit. If a climax could exist in eastern Iowa, it would probably be similar to the climax composed from a number of sites where the trees were old and the stands relatively undisturbed except by single tree deaths. The forest would be predominantly sugar maple with scattered clumps of basswood and oak. Gap-phase species would be predominently boxelder, butternut, black ash, elm, ironwood, and oaks. The understory would be dense with herbaceous forbs, bulbed wildflowers, ferns, and moss. Many of the overstory trees would have at least one large vine attached which is either Virginia creeper or wild grape. Poison ivy is noticeably missing. The forest floor is of the duff-mor type with good organic matter incorporation, moisture, and aeriation. Litter is generally wood debries and maple leaves. Storm-downed or pest-killed trees lie in various stages of decomposition. Decomposition is relatively rapid and recolonization of gaps is quick. The interference is great

from the dense understory and crowded overstory. The trees are crowded and not growing at potentially optimal rates. This "climax" type can and does appear occasionally in moist cove sites in eastern Iowa but seldom holds the site long due to disturbance.

Species attributes

The site preference of red oak reproduction was the more sunny and drier sites than white oak reproduction. White oak reproduction was found in the more moist, shaded areas. Oak was observed to be a disturbance and gap-phase species that depends upon periodic disturbance and/or crown gaps occurring to succeed to the canopy.

Thick hickory stands were observed to delay oak colonization for many years. To manage for hickory, seed tree or heavy shelterwood cutting should be successful. In eastern Iowa, hickory may be moving into some part of the niche held by butternut as the butternut decline progresses. Hickory is also highly interference tolerant for the first few years after germination then rapidly becomes less tolerant. Hickory will grow through heavy understory cover if the limiting canopy is under four feet. Hickory seed distribution must have a large long-range component and/or seed viability over relatively long periods of time.

Ash was observed to maximize its importance successionally in a stand before hickory. Ash will grow through a lot of brush under relatively high light levels. Ash, once established and growing, will dominate a site before oak then will become an escapist and is removed from the site. Ash is a gap-phase species that requires a relatively large canopy gap to be successful.

Elm, cherry, walnut, and a number of other species of the upland forest are generally insignificant on a forest-wide basis. On isolated areas, each may regenerate well, but not successfully over wide areas. The decline and fall of elm in the last three decades has left the forests of eastern Iowa with a large niche space open with no heir-appearant to occupy the space. Successional processes have been greatly disturbed by the elm regenerating profusely but not gaining crown dominance. The elm may completely dominate the understory on a site, and inhibit or preempt the regeneration of other species, but will never grow past the intermediate crown class. The effect on successional patterns is for the elm cycle to be truncated and to hold the site for only a few years. Oak will not regenerate under elm ground cover, but can come in as the elm grows.

Oak silviculture

One generality that presented itself in eastern Iowa was that clearcuts do not regenerate oak. Clearcuts for the most part lead to grass and woody shrubs taking over the site and inhibiting the regeneration of trees. All the clearcuts observed seemed to have microsite extremes of temperature and moisture caused by cutting that inhibited tree regeneration. Patch or group cuttings did regenerate oak and minimized microsite changes. One notable success using small patch cutting was where low levels of 2,4,5-T and 2,4-D had been sprayed on the site. Oak regeneration completely dominated the site.

For oak to regenerate, disturbance of the site was required. Seldom were there enough resources on a site to support oak seedlings unless small or large scale disturbances had occurred in the stand. If a site had heavy sod or a thick litter layer, scarifying the surface would be required to maximize oak regeneration probabilities. Thick litter has wide fluctuations in moisture contents and acts as a physical barrier. The radicles of seedlings could be easily damaged by desiccation. Both sod and extensive litter layers also produce carbon dioxide and ethylene in relatively large amounts, possibly affecting germination and growth of acorns. As sugar maple moves into a stand the

litter layer becomes more continuous and thicker, thus increasing the inhibition of oak regeneration.

Poor sites tend to support oak and ash species in eastern Iowa while good site move toward sugar maple, compositionally. To regenerate oak, the understory needs to be removed on poor sites, while the overstory requires thinning on good sites. The poorer the site, the nearer the ground will be the most limiting layer of interferers. If a site is brushy, the brush should be removed. If the site has established sod, the sod should be broken-up. Brush, once established in an understory or on a clearcut, will dominate the site for at least 25-30 years. With no brush control, on sites that have moderate shrub components, crop-tree rotation may be lengthened by this number of years.

Concepts in regenerating oaks

Observationally, a scenario for regenerating oak was developed over the sampling period in the field. For oak to regenerate, or more precisely, to maximize the probability of oak regenerating in eastern Iowa the following points were critical:

1) an oak seed source is needed from "good" phenotypic individuals.
2) the forest floor cover should be either

bare mineral soil, light grass cover and litter, and/or thin, spotty tree leaf litter.

3) relatively high amounts of direct sun (60-70% of full sun from many sun flecks).
4) minimize interference from the understory.
5) good available moisture.

Maximizing the potential for oak regeneration includes the elimination of grazing predation on the young trees, and strong control of the understory trees and shrubs to favor potential crop species. Overstory thinning may be required where none-layered species cause too great of PAR drop to the understory. Steep slopes at times showed great regeneration. The reason probably resided in the fact that litter layers were non-existent or broken-up and crown coverage was not causing major extinction of PAR due to the staggered crown layers.

In the forest, oak regeneration is occurring beneath crown openings. Oak regeneration is occurring where there is near full sun. Oaks occur where there is little or no shrub layer. Slopes have more regeneration because of breaks in the litter layer and the presence of mineral soil at the surface. Oak regeneration replaces overstory oaks if the understory is slight and the overstory is more open. If

the overstory is too dense, the more interference tolerant species survive. Crown thinning of oak can be benificial or detrimental depending upon the degree of treatment. Heavy crown thinning may allow on-site regeneration to grow into the canopy but may cause some epicormic branching, in early years after the treatment, on residual trees and increased interference from the woody shrub layer. Light crown thinning may not increase the resources available enough for use by the on-site regeneration of oak, but other species reproduction may be favored. Overstory oak crowns cannot fill in canopy gap spaces fast enough to prevent other species from filling the gap. With too much crown thinning, brush and nettles may take over the open areas. If this occurs with no cultural treatment to prevent it, the woody brush can be expected to hold the site away from tree reproduction, for the most part of 25-30 years before tree regeneration or deep woods forbs reoccupy the site.

In the maple stands observed, and where oak was in the stand or in the immediate area, the litter layer seemed too thick and matted for oaks to find a safe germination/growth site. Maple stands also produce a strong light extinction across the canopy. From the stands observed, a scenario was developed for converting a maple stand with scattered oak to an oak stand with scattered maple:

1) remove saplings and pole size maples.

2) remove trees with crowns in direct special competition with oak crowns.
3) repeat in 7-10 years.
4) herbicide the brushy pockets.

On the other hand, if the sugar maple poles and saplings are not eliminated from these stands, events will follow this pattern:

1) sugar maple and oak in the stand overstory.
2) removal of crop maple and oak in overstory.
3) on-site oak and maple regeneration growing toward canopy level.
4) less tolerant species failing.
5) sugar maple stand with scattered oak.

Fire

The idea of prescribed fire is not new to oak management and can be intuitively held to be a destroyer of maple forests and the creator of oak forests. The suppression of fires with the advent of settlement may be surmised to have allowed maple to colonize more areas. Observations of burned areas show that single fires may promote maple stands by stimulating sprouts and regeneration. The periodic burning of oak stands may

promote oak regeneration and prevent maple colonization and distroy maple sprouts. The constant environmental pressure on the maple will eliminate the species from dominating the site. The oak regeneration may be damaged, but to a lesser degree than the thin barked maple. Periodic fire will change the oak forests as we know it to a more open parkland forest with pockets of deep-forest plants as may have been the case before settlement.

DISCUSSION

Introduction

The purpose of an observational study is to put a trained observer into a situation where similarities and differences can be discerned between sampling sites. The act of forcing educated observations to be made over time allows for the production of testable hypotheses stemming from the quantifiable data collected and its analysis, and from the skill of the observer at pattern recognition and definition while all the site factors are impinging the senses. The observer becomes a tool for wholistic viewing of the sampling sites. The result is an integrated theoretical framework, modified by observational sensitivity and education, and supplemented by statistical analysis tools that isolate the effects of specific site factors. In this dissertation, both the theoretical framework of tree and forest growth, and the specific factors suggested to be intimately involved with the control of oak regeneration have been addressed. Each portion is required to understand the significance of the others.

The first part of this discussion section will modify some of the concepts associated with the current biological

and ecological framework of a forest system and its regeneration. The modified concept of the forest, derived from observation on the sample areas and from the literature reviewed earlier in this dissertation, will allow for the integrated understanding of the isolated features examined by the various statistical analyses. The goals of this discussion are a unified view of what controls oak regeneration, a dispatching of forest mythology that tends to inhibit continued silvicultural progress, and a development of integrated forest/tree concepts that allow for better understanding of both regeneration problems and the tree as an interacting organism within the context of eastern Iowa forests.

Development of a basic ecologically interacting unit

Components of phenotype Before continuing, several items need clarification in the context of current forest ecological thought. The first is the role of interference. Interference denotes the actions or mechanisms of competition and allelochemics. Competition is one plant removing or reducing some factor from the environment required by another plant sharing the same habitat. Allelochemics (allelopathy in the broad sense) will be defined here as any effect of one plant on another due to compounds produced and added to the environment.

Allelochemics are not part of competition but one portion of the social component of phenotype. Phenotype is a function of the site component, the competition component, the allelochemic component, the genetic component, and a component-interaction factor. The competition and allelochemic components together comprise the social portion of phenotype. Interference results from the social component, and therefore, is the allelochemic plus the competitive component of phenotype. Rarely are both competitive and allelochemic components of phenotype controlled in experimentation, hence the term "competition" is misused. The term "interference" is the proper term, in most cases, for the species/species interactions found in the literature.

Some tree species, and some genotypes within species, have a greater allelochemic component of interference than other genotypes. Similarly, some genotypes have greater competition components of interference than others. Species use various forms of interference for survival and growth. The competition component of interference predominates in a forest community, with only a few species using a large allelochemic component for interference. The low number of species using substantial allelochemic interference is due to the energy economics of chemical compartmentalization,

self-toxicity, and/or the forgone loss of required resources to highly competitive species. Allelochemics may be a minor component of an individual's phenotype in the forest, yet can be magnified or concentrated at the seed-seedling level and may comprise a greater role in determining survival and growth of a given species than expected.

Sphere of influence A concept from allelochemics worth understanding is the idea of the "sphere of influence" around an individual. The concept of the sphere of influence is derived from eastern philosophies, aikido, and more formally, from Zinke (1962) and Coder (1983). Simply stated, each organism is influenced and influences its environment to a greater or lesser degree. With trees, generally, the larger, more dominant trees will have a greater sphere of influence than smaller trees. Spheres of influence differ from strictly the physical atmospheric environment of the shoots and the soil environment of the roots. Each organism withdraws and deposits specific items into the soil and/or into the atmosphere. The exact composition and degree of these changes are specific to each phenotype in a narrow sense, and specific to each species in a wider sense. This sphere of influence bounds the simplist, ecologically interacting, whole-plant unit in a forest. The use of this concept unifies the allelochemic

and competitive portions of phenotype and more properly integrates all the components of phenotype to allow for determinations of biophysical and biochemical interactions.

Fiefspace concept By using the concept of sphere of influence, species and site interactions can be more clearly understood. The individual, surrounded by its own sphere of influence, comprises and influences a "fiefspace". The building blocks of the fiefspace concept has been derived from the general works of the authors in the literature review section. Specifically, Horn, Feet, Christensen, Grime, Doyle, Loucks, McIntosh, Shugart, Soloman(s), Connell, Slatyer, Cottam, Lorimer, West, Fice, Whittaker, and Shigo all provided the foundation, coupled with selected Iowa State classroom lectures by Schultz, Scholtes, Shaw, Pavlik, Blackmer, and LaMotte, for further explorations.

Fiefspace includes both the organism and the dynamic area surrounding the individual wherein the predominant life-force and the major influencer of resources is that organism. Fiefspace includes an area beyond the structural portions of the organism. Fiefspace is the sheath of space around a tree influenced by that tree through complex boundary layer, rhizosphere, and resource preemption interactions. For example, the prime resources on a site are available water, carbon dioxide, mineral nutrients, and

photosynthetically active radiation. The tree fiefspace that controls or influences the most of these substances in the correct proportions, over time, will grow the fastest. Considering photosynthetically active radiation, large trees will intercept light energy, act as a selective filter, and preclude energy input to lower fiefspaces. The drop in energy levels (i.e., the light extinction curve) forces other trees to make physiological-architectural adaptations in their fiefspaces to lower light intensities, accept static fiefspaces (shade tolerance), or do nothing (death). As long as the resource building blocks are available in a fiefspace at greater than continually increasing maintenance levels for a stem, carbon will be fixed and moved into fiefspace expansion activities. A large tree's fiefspace will exist below the photosynthetic array for some distance from the crown, branch, or leaf due to energy consumption or preemption. The area directly below a large leaf, normal to incoming direct beam photons, is nearly as totally biologically influenced as the space in which the leaf actually resides. This area of influence is a part of fiefspace.

In a two-dimensional diagram where trees are considered idealized portions of differing sized cylinders standing on end, fiefspace can be represented as various sized circles,

horizontal to the ground, each denoting the fiefspace size at a given height within the stand. If a slice was taken through a stand at a specific height above the ground, circles could delineate the extent of all fiefspaces. If the slice was taken over the site at the traditional codominant crown level, there would be many large circles where the codominant crowns reside, some smaller circles where the very tops of the intermediate tree crowns occur, and smaller circles where the lower crown and bole areas of emergent or dominant trees occur. Moving up or down, above or below the soil surface, would cause the circle-sizes, which represent the maximum fiefspace extent of an individual stem, to change rapidly, either growing, shrinking, disappearing, or appearing. If you could stack an infinite number of of these circle diagrams upon each other representing fiefspace extent at all levels in a stand, and still see through the stack, you would behold the realm of fiefspaces for a forested site at one single moment in time. If a stack of circle diagrams could be assembled for each moment over 500 years, and each photographed with a motion-picture camera one stack of diagrams per frame, the final product would be a motion picture showing the dynamics of forest-system fiefspaces or spheres of influence. The control of physical space and its resources is the ultimate

response for the genetic survival of a species, given that all other species use the same general physiological tools and are subject to roughly the same constraints.

Remember that here is presented an idealized view of fiefspace. Fiefspace is actually the sheath of space around the tree and therefore, each individual limb, leaf, and bud has not the idealized circular space in which it influences and is influenced by its surroundings, but a highly convoluted and lobed fiefspace area. Fiefspace is highly dynamic and changes size over seconds, diurnal cycles, and years. The interaction between the tree and its environment at any given time will determine the instantaneous size of the fiefspace.

Life/death of the tree and its fiefspace The most critical portions of tree fiefspace existence, from a regeneration standpoint, is the initial expansion and the final collapse. Foresters have traditionally been well-schooled in the fiefspace stages of continual, rapid expansion, or the straight-line portion of the S-curve growth function. There are ecological-growth models to move the trees through time to biological maturity once they are present and established. Beyond a certain fiefspace size, depending upon species, fiefspace expansion is inevitable due to resource capture, if physical, chemical, biological,

and anthropological factors do not catastrophically intervene. To summarize, once past a certain point, tree growth is a function of the natural efficiencies of resource capture.

A little less is known about the initial expansion stages of tree growth. This is where fiefspace is expanded by superior phenotypic responses or, as is usually the case, by default. All responses to external and internal stimuli are fixed at the time of conception by the genotype, except for occasional semi-random rearrangements. Programmed fiefspace expansion is a step-by-step process where failure of any step destroys the sequencing of biological events whereby new outcomes will most probably lead to death. Relative scale is important in this discussion especially at the seedling level. Scale differences between a fiefspace of a year-old seedling relative to its site is great compared with the differences in scale between a 200 year-old dominant canopy tree's fiefspace and its site. The initial sequencing of fiefspace expansion versus site interactions requires much more study.

The other critical point of tree growth, and the final thermodynamic solution to biological carbon fixation, is electron equilibrium in a highly oxidative environment. Little knowledge is available about the over-mature and

dying tree. The erosion rate of fiefspace should generally increase with time until a point is reached where maintenance requirements, already cut to absolute minimums, cannot be met. The symplast/apoplast gradient of electrons will be greatly decreased because of flows (i.e., shorts) around the biological electron dams and generators used to power the tree system. Death, however, does not eliminate fiefspace. Space is still being occupied and latent chemical reactions may still occur.

Fiefspace just before and after tree death does shrink rapidly. Fiefspace shrinks before death by the tree withdrawing from heavy interference territories, and therefore, some of the electron resources of the tree are left behind, outside the living system. This is accomplished by internal compartmentalization of those areas requiring large amounts of electronic input. Less efficient portions of the tree system are shut off. The maximum size a fiefspace ever reaches may predispose the tree to a fast or slow loss of fiefspace in the end. One-time large fiefspaces may collapse faster than small fiefspaces when the tree declines and dies.

With declining fiefspace, electron-rich materials are biologically cut off from the tree, providing potential energy for other organisms. The compartmentalization, or

contraction of fiefspace, is only a temporary solution for responding to neighboring fiefspaces and internal resource economics. The compartmentalization and maintenance costs will again become too great and somewhere, maybe associated with another organism consuming an area, the final electronic barriers created by biological molecules will collapse. The initial flush of electrons may end quickly, but the electron trickle continues for years, still maintaining some portion of the fiefspace of the old occupant.

The reason that tree establishment and death have been reviewed here is because it is at this step that managers have the least control. In fact, the idea of germination/establishment and death at two separate points at opposite ends of a continuum shows our innate interest in only the rapid fiefspace expansion stage of tree growth. In the forest there is actually a circle of death, germination, establishment, growth, and maintenance in which foresters have traditionally made a conceptual break between death and establishment. Actually, these stages can be considered one period in a stand when resources are made available for the potential change or creation of fiefspace. This period of resource availability is critical for regeneration.

Resources and fiefspace While tree fiefspaces are being rapidly expanded and there is much interference between individuals, few resources are available for new reproduction in an area. Resources not being used, or resources having recently been released from domination, allow new fiefspaces to be started or expanded. Rapidly expanding fiefspaces can inhibit and/or dominate neighboring fiefspaces or even the potential sites of fiefspace establishment. Within a dominant fiefspace, other fiefspaces usually get started or expand only before or after the major expansion stages of the site dominator. An exception is where new fiefspace expansion is located on the edge between dominant fiefspaces where some resources can be usurped. The period of tree dying and death, whether natural or as a result of a cultural treatment, is a major adjustment period for local fiefspaces and a period of initiation (establishment) of new fiefspaces. Foresters must work to maximize crop tree establishment and fiefspace expansion during this period.

Fiefspace can also be viewed from a site expansion point of view. Fiefspaces can be microsites at the level of a seed or seedling. Fiefspace will not stay at the microsite level. A given dominant canopy tree fiefspace may contain hundreds of specific microsites. Microsites are

potential sites for growth and development. A fiefspace may begin by occupying a general microsite but will quickly expand to encompass many microsites if allowed. To clarify, the forest floor has many microsites capable of allowing germination. Of the sites where germination is allowed, some fraction of those sites will allow establishment of the seedling. These establishment sites will be made up of only a few sites where the seedling can dominate the site. These dominance sites are where the sphere of influence of a tree has expanded enough (i.e., the tree has grown enough) so the dominant organism on that specific site is the tree. The decline in absolute site numbers from safe sites to establishment sites to dominance sites is the mortality rate and is controlled by biotic and abiotic microsite/site characteristics.

The fiefspace of one tree may exist within the fiefspace of another, thus the name. Because of competitive and allelochemic effects, the larger and taller trees will be the dominators of the site. The top level, or ultimate controller of the largest fiefspaces on a site, are the "drymanax" trees (from the Greek for "king of the forest"). In the forest, these trees are equivalent to trees in the codominant, dominant, or emergent crown positions. The drymanax trees can dominate the physical, chemical, water,

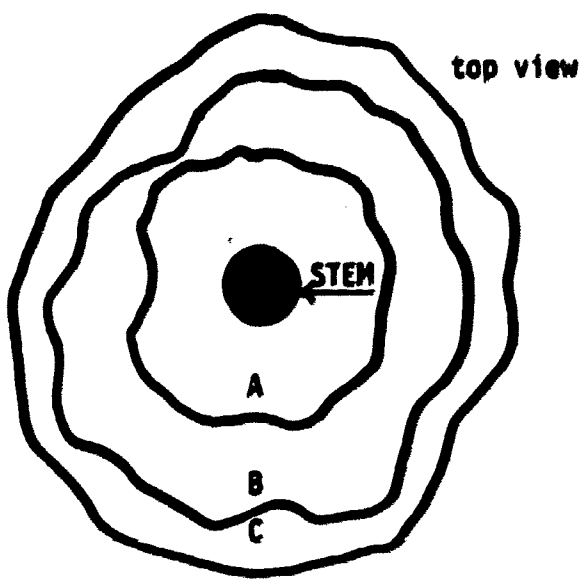
nutrient, and energy resources of the site, and resource recycling. In traditional forestry terms, drymanax trees should correspond to the crop trees that eventually will be harvested. The size of the major fiefspaces for a given mature timber stand is the maximum area each drymanax tree can dominate above and below ground. Fiefspaces below ground are generally larger than above ground on a distance from the stem basis. It is the drymanax trees that most strongly control potential regeneration on a site.

Spacial and successional relationships The fiefspace around a tree, above ground, is shown in Figure 17. The interference areas (spheres) around the tree are; a) dominance (i.e., sole interferer), b) codominance (i.e., several interferers for resources), and, c) combative (i.e., many potential interferers and great resource availability). The relative size of each interference area can change with time and with species. The sizes of the interference areas change with inherent crown form. late-successional species tend to have small dominance and combative spheres. Excurrent growth-form hardwoods will tend to have large dominance, but small codominance and combative spheres. Extremely shade tolerant trees, such as ironwood (Ostrya sp.) will have a fiefspace comprised almost totally of a codominant area and be tolerant of drymanax tree

interference. Early-successional species will tend to have large dominance and small codominace spheres.

As a simplified example, Figure 18 shows the above ground fiefspace differentiation occurring between four trees of two species. The combative zone may be the ideal location for the growth and regeneration of other trees due to the lack of any species obtaining dominance and therefore, lack of resource preemption. Also, the combative zone will be much larger between two trees of the same species than two trees of different species. Combative zones in the forest are actually transient and develop into codominant zones with time as near-dominance for the resources present is reached. If an individual establishes itself in a combative zone, that area may become the dominance zone of that individual with time. A rule of forest tree life is: The tree which cannot dominate will be dominated. Therefore, succession is the result of compositional movement and selection toward higher resource efficiencies.

Early-successional species (in secondary successional roles) will dominate a site weakly, die in response to stress from resource use, and do not chemically alter the site to any great degree. These species have little genotypic response to the combative stress present as the



A = dominance
B = codominance
C = combative

FIGURE 17. Interference areas or zones of a fiefspace around a tree stem above ground

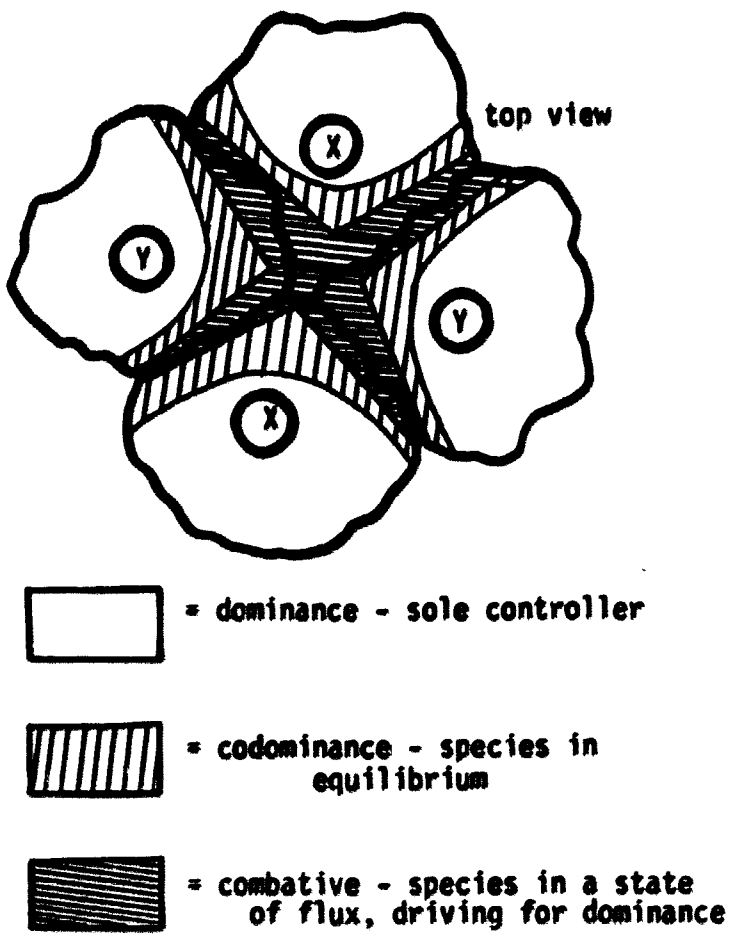


FIGURE 18. Example of interference zones between tree crowns

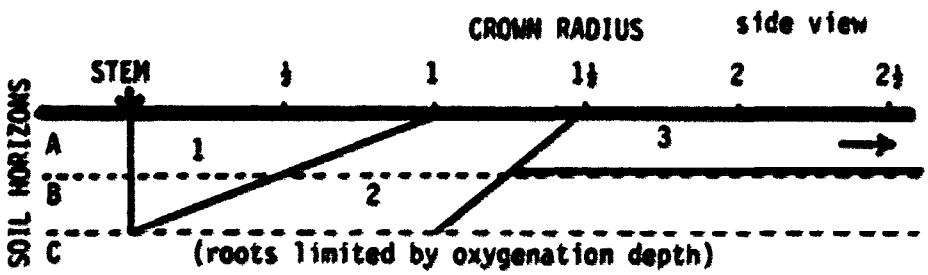
site becomes more fully occupied and fiefspaces expand and greatly overlap. The early successional species rely on rapid resource acquisition and generally tolerate large fluctuations in fiefspace. late-successional species, on the other hand, dominate the site strongly, survive being severely stressed by the lack of resources, and chemically alter the site with time. These species are able to genetypically respond to combative stress for resources. late-successional species are relatively slow at resource acquisition and systematically reinforce fiefspace expansion by their growth rate and form.

With the specification of these rules, an exception must exist. There should exist super-competitors that can withstand combative stress, do not chemically alter their sites to any great degree, and systematicly expand their fiefspace. Some earlier-successional species in high water environments or trees on sites where the climate is highly stable would probably meet these requirements. The trees of late-successional tropical forests could be examples.

The sphere of influence below ground differs from the above ground sphere due to root anatomy and morphology, environmental and physical constraints of the site, and the interactive control relationship with the shoot. Figure 19 depicts the sphere of influence zones around a tree below

ground. The relative distances in this figure are based on crown radius to provide some frame of reference. Actual below ground interference zones will undulate in depth and radius from the tree. The zones shown in Figure 19 do not allow for the conceptualization of the true nature of the function and appearance of the tree root system. Zone 1 is the mechanical zone, responsible for mechanical support and water uptake. Zone 2 is the intense competition zone. Zone 2 is slowly expanded over the life-span of the tree. In zone 2, the tree roots are under the most substained interference from roots of other neighboring species. Zone 3 is the cohabitation zone. Roots here are predominantly of the "rope-sized" feeder system type that occur over specific limited areas at some distance from the parent tree and may cross or be within other fiefspaces. This zone may have strong root-root interference and generally contains fans of feeder roots in patches which may or may not be interspersed with roots and feeder fans of other individuals. Feeder root fans can also be found in zones 1 and 2.

Within the root zones, the chances of new reproduction becoming established increases with distance from a tree. In the traditional sense of tree dominance, a dominant and codominant tree will occupy, or tend to have a sphere of influence (fiefspace), that will contain all three zones.



1 = mechanical zone
2 = competition zone
3 = cohabitation zone

FIGURE 19. Root dominance zones within the fiefspace of a tree

Intermediate trees will tend to have fiefspaces concentrated into zones 1 and 2. Suppressed trees will tend to have fiefspaces with primarily zone 1. Regenerating species must germinate, then expand their own sphere of influence usually within the fiefspace of another tree. Trees will genetically vary in the proportion of space allowed in each root zone depending upon site constraints. For example, stress tolerant species tend to establish a strong first zone (mechanical zone - taproot) then proceed with strengthening their hold on the site. Highly competitive species tend to establish zones 2 and 3 first (fiberous root system), to start gathering resources, then continue to expand zone 1. Rooting types can mirror the phenotypic emphasis the tree places on relative resource value, with the continuum ends comprised of space occupiers and resource gatherers. In closed, overstocked stands, the root area of a tree may progressively occupy less and less space. Dominance is reached by the tree that can maximize its fiefspace, in general, and root zone 2 in particular.

In a tree, roots are opportunistic interferers. The crown is more passive in its interference, utilizing long/short shoot growth. A major function of the roots is to procure nutrients for the tree. Nutrients cycle within the fiefspace and across it. With succession, nutrients are

continually redistributed and compartmentalized in the biomass of the community. This community compartmentalization is most strongly developed in late-successional forests. Fertilization may pressure the community to hold its current successional stage or to move backwards, if nutrients are the major limitation on the site.

Early-successional communities tend to be adapted for physical environmental inputs, while late-successional communities tend to be adapted for more biological environmental inputs. From a succession point of view, the early-successional species start the cycling of nutrients and the biological interaction with the soil. Late-successional species will continue to compartmentalize nutrients in the biomass. For example, early-successional species do not strongly conserve nutrients internally. Late-successional species use a strong internal cycling of nutrients for conservation and/or preemption. Once a nutrient moves beyond the symplast, it is beyond direct biological control. The lack of resource influence is a characteristic of early-successional stands (from Etherington, 1982; Horn, 1974; Bartour et al., 1980; Parrish and Bazzaz, 1982; Drury and Nisbet, 1973).

Fiefspace size The fiefspace of a tree may increase or decrease in size with time. This increase in fiefspace size is usually positively correlated with growth (net electron and carbon gain), but may not be proportional to growth, depending upon the interactions with other fiefspaces. As time progresses in an even-aged stand, and mortality continues within the stand, a relatively greater proportion of the resources on a site can be released upon the death of a single individual. For a tree to have grown into the canopy at all, its fiefspace must have been expanding at some point in the near past. The fiefspace of a tree, upon continual interference, will reach equilibrium, then will slowly decline in size until death, when the fiefspace will rapidly shrink. The shrinking of one fiefspace can be much faster than the subsequent expansion of other fiefspaces around the area, especially in late-successional stands, therefore a combative zone is formed from the resources being released or not preempted. The increased resource levels can allow other individuals to become established on the site or allow suppressed seedlings to rapidly expand their fiefspaces. Figure 20 shows the idealized fiefspace expansion of dominating individuals over time, with inherent mortality, causing absolute numbers of individuals to decline. As each tree's fiefspace becomes

larger, it becomes more of an energy cost for the tree to expand its fiefspace and to preempt the resources resulting from mortality on the site. As tree fiefspaces become larger, more regeneration in the stand may be possible. Within a fiefspace, resource efficiency may become greater, while between fiefspaces, resource efficiency declines due to physical-environmental limitations on tree growth and form. Of course, within the forest there will always be nested sets of fiefspaces, not one single size group at a time to account for.

Each species has a characteristic, physiologically limited, fiefspace size. Later-successional species will tend to have progressively larger potential fiefspaces than most early-successional species. But, the larger potential fiefspaces of late-successional species may allow a greater chance of reproduction in the stand. Some species, however, have such a dominating effect that their fiefspace expansion is literally overpowering and they can cause an acceleration of changes in a stand leading to complete species conversion. Sugar maple/black maple could be considered such a species. Exceptions to the rule of larger fiefspaces being associated with later-successional species also can be found in the excurrent growth-form hardwoods that have smaller, above ground fiefspaces, and in any species that

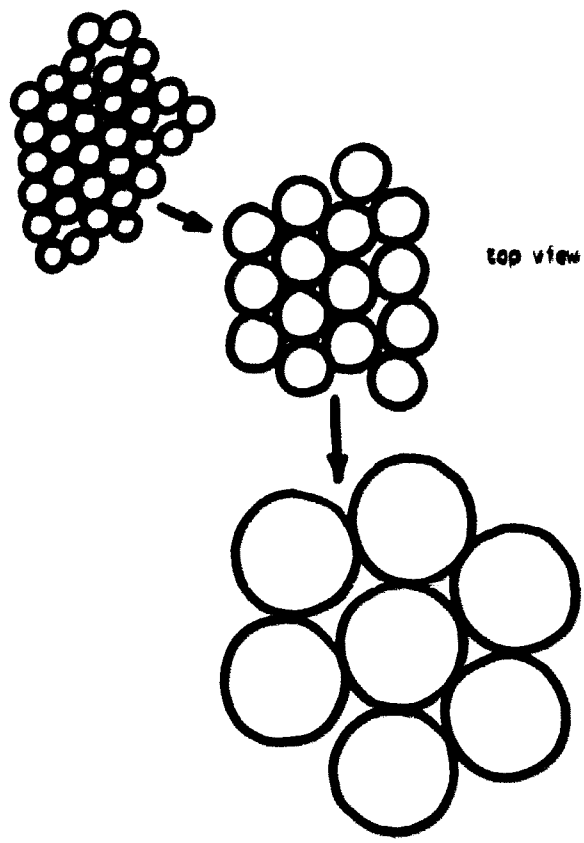


FIGURE 20. Idealized above-ground fiefspace development over time

have relatively large allelochemic components of interference. For example, walnut has a small above ground fiefspace but maintains dominance and large below-ground fiefspace by a large chemical interference factor.

Domination of a site comes from influencing a large fiefspace. Late-successional species have large fiefspaces that are maintained by the monolayered photosynthetic array form. Where there are species with large dominance and small codominance crown zones, a multilayered growth form will be expected to maximize light resource efficiency. Small dominance and large codominance crown zones will be expected to lead to a monolayered photosynthetic array growth form.

One interesting effect seen in trees is stagnation. Early-successional species cannot truly stagnate. Some individuals will eventually dominate the site due to high levels of intraspecific competition which causes the stand to break up. Once one individual gains a small advantage in fiefspace, the advantage will be magnified and continue to accelerate. Late-successional species can stagnate in a stand because each individual can survive the high stress of intraspecific interference by maintenance growth rates and low resource requirements until times are favorable. No dominance of the site is attained because no individual is

genetically equipped to invest electronic potential to spurt ahead of any other individual, assuming no major microsite differences exist. Early-successional species respond to stagnation by death and late-successional species respond to stagnation by growth at maintenance levels as would occur in an understory. "Early-successional species" are early-successional species because they cannot grow for extended periods of time in a static fiefspace situation and cannot survive resource preemption stress.

Tolerance factors

Another point to clarify concerning tree regeneration is the concept of shade tolerance. A difference must be made between initial tolerance and continual or dynamic tolerance. Under constant conditions that are limiting, and in an area where all germinating seeds become established, the survival curve for seedlings will drop rapidly over a short period of time following a traditional reverse-S-form population function. Up to the time of the increased rate of mortality, individuals are being lost slowly. Finally, when the individuals are no longer able to maintain an existence at the given resource input level, they perish.

The minimum light levels required over time for two species will differ over the short and long run. Initial

shade tolerance for a species is the relative resource level required for approximately the first year of life. Continued shade tolerance levels over time, between species and within individuals, depend upon other resources present on a site and individual growth form. Waiting on a site, by growing at maintenance resource levels, does not insure eventual success. Shade tolerance then, is not a case of static tolerance levels at one point in time, but a dynamic residence time at a given resource level. Residence time at a given resource level can be determined from time zero to the point of the rapid mortality increase for a population of even-aged seedlings. Residence time can be modified by changing resource levels and growth form.

Over time, it will take more and more light to keep a given individual present on a site if the light resource is limiting. The time after the initial germination and establishment period is the dynamic shade tolerance period of a species. The initial shade tolerance level is the amount of light needed for germination, if any, and for utilization of seed materials (at least one year). The dynamic tolerance level may not change significantly from the initial tolerance level, but will tend to move toward greater resource requirements over time due to resource starvation caused by required fiefspace expansion. This

concept can also hold for other resource tolerances. Tolerance effects, coupled with good dispersal, are the reasons cherry, hickory, and ash occur throughout the forests of eastern Iowa in such profussion but do not occur raspantly in the main forest canopies.

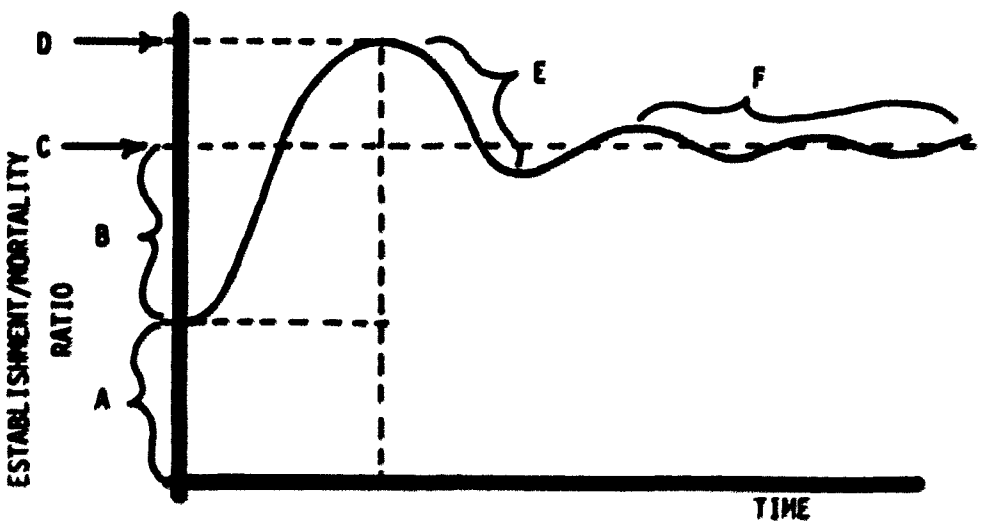
Establishment/mortality rates

A final point for reflection is species establishment and mortality rates on a site based on the general productivity curve of Bormann and Likens (1979) (Figure 1). Figure 21 shows an establishment/mortality ratio for a stand following disturbance. The curve has several components. Note the curve slopes, which are relative rates, the maximums, minimums, and the initial starting point of the curve. The highest point on the curve will occur when a majority of the trees on a site would be starting into their rapid growth phase, under an even-aged system. The increase in mortality among the tree reproduction would occur throughout the rapid growth phase of the larger trees on the site. The curve will level out as the trees reach phenotypic maturity. The oak stands in eastern Iowa are nearing the pinnacle of their rapid growth phase on the basis of average stand ages, and therefore, the lack of regeneration at this time is not unexpected, ecologically.

Controlled harvesting can provide the resource influx for initiation of site regeneration.

Model Constraints and Ramifications

With a better understanding of the forest, we can return now to the ramifications of the regeneration model (Figure 2). The model is a summation of factors affecting regeneration. The climatic and seed dispersal components can be gleaned from the literature for the most part. Tree presence on the site and the regeneration can be easily determined. The site and social factors are more difficult to approach because of the large interaction component between specific factors. If one can measure the proper controlling site or social factors, and find its correlation with regeneration, a model can be used to conceptually manipulate the components of the site to maximize regeneration of a particular species. This process was attempted in this dissertation for eastern Iowa forests using several model assumptions. One assumption was that density variables and relative growth functions estimated from these data were the only factors from the social component needing to be determined. The rest of the social component will be considered to be the same over all stands.



A = potential for asexual reproduction

B = long term sexual addition to reproduction

C = long range regeneration equilibrium

D = peak establishment dominance and maximum regeneration

E = initial mortality dominance

F = damping of regeneration and mortality cycles to reach study-state

FIGURE 21. Graph for regeneration and mortality in a given stand (gap) over time

The second assumption was that we were measuring the correct characteristics on a site that affect regeneration. Obviously, both assumptions are prctatly incorrect, but both can be reapproached in other studies which emphasize these specific items.

For a given micrcsite, by using this model, one should be able tc determine the regeneration that will succeed. Under ideal conditions, this would te true. Because of the limitations in the data set, we must settle for an estimate. Any estimate we make must be a prctability for regenerating the microsite with a particular species. From the model, and from field information, it ic clear that any species can regenerate on a microsite at any point along the traditional successional patterns. There is nc magic that prevents cottonwood, for example, frcm germinating and growing cn a microsite beneath a sugar maple stand. Because of species and site factors, the probability is extremely low, and decreases the longer the cottonwood seed or seedling is present. But at no time will the prctability be zerc. It becomes clear that oak reproduction management is a process for trying to maximize the probability cf regenerating oak while minimizing the probability cf regenerating cther species on a given site.

As a stand ages, changes occur in tree composition (succession) and in associated and unassociated site, climatic, and social features. In other words, throughout succession, the regeneration probabilities for each species are changing. To illustrate this point, see Figure 22. Each species is represented by a seperate curve. The curves become progressively lower and more extensive with time. Notice point X in Figure 22. At point X, all species have some chance of regenerating. There are one or two species that have the greatest probability of regenerating while the other species have lower probabilities. Part of the variation apparent in the field is a function of having a low probability species occurring. The chances may be great that some species will not regenerate on a site, but that does not preclude the possibility. Field data show that there is no facilitation order that is strictly held to, but there is a probabilistic order where, of all microsites, some will contain the low probability species. Figure 22 can also describe what may occur at harvest time using various cutting techniques. The more one cuts, with the maximum limit being a clearcut, the more the site probabilities for regeneration change (moved toward the left in Figure 22). The size of the cut can also change regeneration potentials by affecting many of the components

of the regeneration model. Another major point is that closeness of a species to the disturbance area and the ability to vegetatively reproduce will magnify the regeneration probabilities of that species.

An interesting result of building probability curves is the role of the super-tolerant species, such as ironwood or dogwood. If an ultimate climax could exist, these two species should be the dominants. Their regeneration probability curves would be low but very drawn out and extensive compared to other species over the long-run. Depending upon their inherent establishment/mortality rates, these species could exist as dominants that completely control a site due to relatively small physical dimensions. The small physical size would allow higher effective densities for resource preemption and a decrease in gap size, functionally eliminating invasion by gap species. The probability of regenerating a super-tolerant species might be confounded by the requirement for mutualistic associations.

A probability curve set based on the field data could not be produced for the eastern Iowa forests from this set of data since that was not the purpose of the experimental design. The conceptual integrity of the model can provide better insights into the forest and its regenerative

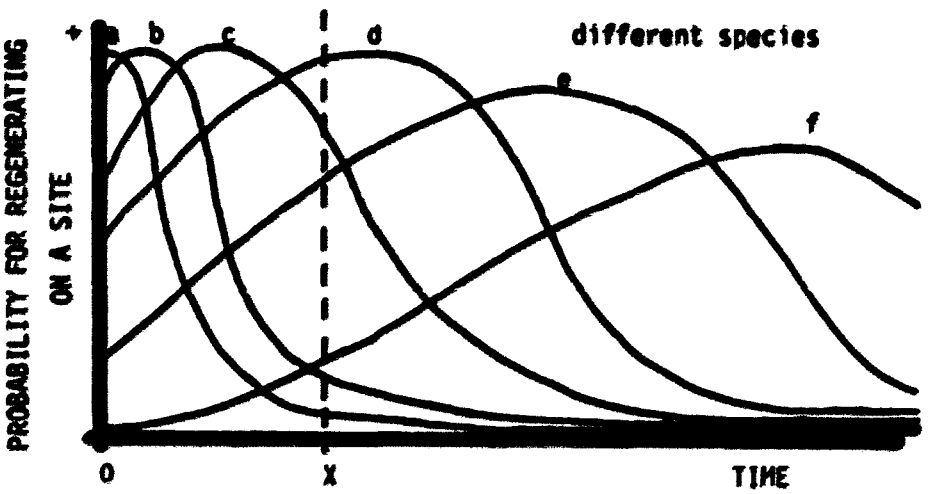


FIGURE 22. Regeneration probability changes over time where zero time is total disturbance of the site

variation over time and from place to place until the "real" dimensions of the probability functions can be determined.

Development of Model Applications

Introduction

The information gleaned from statistical analyses and observations can be combined to realize some level of understanding about the oak regeneration problem. Guided by the preceding conceptual framework, the statistical analyses helped to define the limits of regenerative characteristics, given the inherent weaknesses of each analysis tool.

A point to reflect upon concerning the entire data set is the low linear correlations of single variables to oak regeneration stocking and survival values. The data variance and plotting show there are probably also low curvi-linear correlations of single variables. This apparent lack of substantial relationships between regeneration stocking and survival, and single variables, suggest two alternatives. The first alternative is that the wrong variables were measured. With poor variable selection, strong relationships would not be expected. The presence of some correlation could be due to chance or measurement of a variable that acts as a poor approximation

of a "true" variable strongly correlated with oak regeneration and survival. This alternative is difficult to accept completely because past work with other species of trees and with oak has shown strong relationships existing between some variables and reproduction. Many of these variables were measured in this study. If oak behaves as other tree-forms, variables affecting one species or population may be assumed to have some type of affect on oak. Oak is not so differentiated genetically that its physiological features deviate immensely from other species. The effect of one factor can be expected to vary by its degree of effect rather than by the presence or complete absence of an effect. Therefore, alternative one is probably not the case here, given the current information on the ecology and physiology of oak.

The second alternative is that the correlations between single variables and oak regeneration do suggest the "true" relationships occurring in the forest. If this was not the case, and a single, highly correlated variable was present, past and present analysis should, at least, have approximated the relationship. In support of this alternative is the past poor regeneration record within oak stands, especially in eastern Iowa, and throughout the oak cropping area of the eastern United States. Management

guides have attempted to insure reasonable chances of regeneration success, but applications have yielded highly variable results. There is an oak regeneration problem as shown by the existence of the multitude of papers and conferences on oak regeneration in the last decade. The oak regeneration answers, for the most part, remain elusive. A possible explanation of oak regeneration problems lie within the linear correlation tables. The variables measured are generally representing a site effect that does impact oak reproduction but with a low linear correlation. An effect by one variable can be wholely or partially overshadowed by the effect of another variable.

Invoking Liebig's law of the minimum, oak reproduction is occurring in a forest environment where there are many constraining variables or minimums. Each constraint also interacts with other site and biological factors. Because of the multiple site constraints and their interactions, variables may approximate one constraint and its interactions over only narrow regenerative limits, while reproduction is rapidly constrained by other site or biological factors. This would lead to the low linear correlations between variables and reproduction. Therefore, the second alternative will be accepted.

Acceptance of the second alternative for the relationships between single variables and regeneration calls for a intuitive change in data analysis. The change is from looking for several highly correlated site factors to viewing variables in groups, or as composite factors. Scenarios can then be produced that will account for regeneration variance while not moving beyond the natural constraints of the forest understory. From the analyses, picking the major constraining factors that arise, and then fabricating a biologically based scheme for dispersing, germinating, establishing, and continually growing oaks while minimizing any constraining effects, can lead to testable hypotheses. Within the relationships of variables and regeneration are suggested the constraints on oak reproduction. Knowing the nature of any constraints can then lead to methods for circumventing or minimizing constraining effects to reproduce oak. At the low correlation levels encountered in this study, the background "noise" of variable interactions and marginal relationships had to be stripped from the important relationships. The development of a scenario that works to regenerate oak from the vantage point of several seperate analyses helped to identify the important oak regeneration factors. The following paragraphs will identify some of the important

constraints of oak reproduction and propose a scenario that should increase the probability of regenerating oak in eastern Iowa.

The important regenerative constraints on oak

Numerous analysis techniques were separately utilized to insure that the true nature of the oak regeneration problem was being approached. It should be remembered that all sites sampled were required to have oak reproduction present, and therefore, this study is not representative of all forest "types" of eastern Iowa, just sites that were regenerating oak. Also, the management assumption is that oak is the major product choice of the landowners now and into the future.

Upon examination of the results from different analyses, several oak regeneration attributes and constraints could be identified. The first item of note was the regeneration group acting as a major interferer with the oaks. The regeneration group most predominantly involved with interfering with oak regeneration is sugar maple. Functionally, none of the other regeneration groups except sugar maple have a large enough importance component on sites reproducing oak stems in eastern Iowa to interfere with the oaks except on a small scale and in isolated

patches. Tables 40 and 41 both suggest that sugar maple has large importance levels in the oak stands. Citing the regeneration importance numbers (Table 46), the red oak and sugar maple are at similar regenerative potential levels while white oak still maintains a slight regenerative advantage in the stands, once each is established. By using the regeneration importance weighting method (Table 48), the regeneration occurrence values for each regeneration group becomes more heavily in favor of the sugar maple group with red oak, in particular, continuing to lose importance in the stands.

Examination of the information in Table 45 suggests that with increasing regeneration diversity on the site, which should signify greater resource availability, that oak is becoming less important while sugar maple is gaining in importance. On sites where some limitation pressure is acting upon maple, oak can maintain itself. This idea is also shown in Figure 12, the successional flow diagram. In Figure 12, the movement of the stands toward sugar maple could be slowed or stopped by putting an anthropological stress on the maple while favoring the oaks. This action would maintain the oaks as dominants on the site while eliminating or minimizing their major interferer. From Table 50, the steady-state composition level of the forest,

accepting the assumptions involved, will compositionally approach almost half sugar maple with white oak and red oak still present in the stands. Over the short-run, if maple is stressed, the red oak - white oak regeneration group can maintain its stand importance or expand into other sites. Great enough stress put upon sugar maple will increase the importance of red oak in the stands while, at least, maintaining white oak. Stress from cultural treatments is required because (Table 51) about 60% of the sites are already "locked into" a succeeding regeneration regime. The sites that are moving toward sugar maple could have their relative compositional change velocities slowed or stopped by cultural means, thereby allowing for the potential change of their understories over time, assuming adequate resources were made available. Other sites that are moving toward oak could be reinforced or accelerated along their compositional change vector by resource availability increases from cultural treatments.

With the invoking of "resource availability", a point about cultural treatments of the forest must be made. Regeneration management is the modification of the resource environment, thus the fiefspaces of crop-species. At the mean age of the current stands in eastern Iowa, given the site and climatic factors involved, more and more resources

are becoming available (i.e., not being preempted from use) that will allow for the establishment and expansion of fiefspaces. The eastern Iowa forests seem to be at the pinnacle or beyond on the curve in Figure 1, on the basis of stand ages. As the forest of eastern Iowa becomes older, this process of resource availability will increase. Unfortunately, due to physiological constraints on oak (interference tolerance), the sugar maple is presently reaping tremendous colonization advantages. As the resources continue to increase in availability to a point where the oak can utilize them, sugar maple will already be entrenched in the understories and usurp any available resources. Without the sugar maple present, the oaks would replace the oaks. With sugar maple present and in position for utilizing additional resources that become available, oak regeneration will be minimized. To reverse this process, oak fiefspaces must be favored to provide for establishment of and movement into the rapid growth phase while at the same time eliminating maple fiefspaces. In summary, each site will have a given productivity (i.e., available resource levels) that will support a given number of fiefspaces. Poor sites will support fewer fiefspaces than good sites. To manage regeneration, the resources that each site has must be manipulated so that the crop-tree fiefspaces are the beneficiaries.

In eastern Iowa forest stands, the battle for most of the resources is between sugar maple and oak (Table 53). Further analysis suggests that the oak is being replaced or interfered with by sugar maple, not the other way around. The oak is not interfering with sugar maple, but is being eliminated by the more efficient fiefspace establishment and expansion patterns of sugar maple (Table 56). Every other analyzed regeneration group, except ash, is more tolerant of general interference than oak (Table 55). Oak is also interfered with by many more regeneration groups than is sugar maple (Tables 57 and 58). The result is that oak is not a good interferer, and with its local seed dispersal, does not colonize promiscuously.

There is little difference between the site extinction properties of the oaks in relation to the sugar maple (Table 29). Both groups maintain themselves in the understory well. Maintenance in the understory can also be a function of the vegetative reproduction of a stem. This discussion has emphasized seedling establishment and growth, but differential vegetative reproduction could lead to the same types of compositional and interference effects within these forests.

Table 31 gives the critical diameters found for the oaks and the sugar maple. White oak regeneration stems have

the best survival chances, based upon this measure, among the three regeneration groups. Once white oak stems are beyond 6.2 cm, red oak stems are past 7.4 cm, and sugar maple stems are past 8.7 cm in diameter, each have a high probability of surviving in the stand and potentially gaining the canopy. This measure could be inferred to approximate the minimum fiefspace size required to start into the rapid growth phase. Regeneration management should intensively attempt to produce stems up to this size. Afterwards, much less cultural input will be needed to expand fiefspaces. Unfortunately, from an interference standpoint, red oak is one of the slowest growing regeneration groups in the forest for the first few years (Table 30). If the fiefspace expansion activities of red oak can be maintained, it does eventually increase its relative growth rate. Of the regeneration groups analyzed, the oaks are the best at fiefspace expansion over the long-run. Of course, the fiefspace expansion attributes of 15-25 year old stems does little if the 1-7 year old stem growth is poor, as in red oak, or if the stem is stifled by interference. In this regard, white oak is well-suited to the forest areas studied because of good fiefspace expansion attributes. Red oak, on the other hand, is the regeneration group most potentially limited by the first 7 years of

growth. It is the first 7-10 years of growth in the stand then, that "sorts out" the eventual dominants on the site. Fiefspace expansion activities during this period strongly determine later success (Figure 9). Intensive regeneration management will be required in the first 7-10 years of the stand with periodic resource allocation changes made thereafter to maximize crop-tree fiefspace expansion.

The constraints on oak regeneration establishment are given in Table 24. The constraints can be summarized into several points. The first and most critically important point is that oak regeneration is limited predominantly by resource interference in eastern Iowa forests. Sites that are more productive, with correspondingly more interference, will tend to have oak becoming less important over time. The second point is that of the constraints identified, only a few of them can be manipulated by a regeneration manager. Of those few constraints that can be manipulated, it is the resource availability constraints that affect oak regeneration the most. The suggestion given by these analyses, and from the literature, is that the site acts as a maximum limit of total fiefspace area, with the interactions between fiefspaces limiting the reproduction. The major interference constraint could be minimized by removing photosynthetic arrays and associated fiefspaces,

especially below 4.5 feet (1.37 m) from the ground. To increase the probability of oak regeneration, resources should be released, or the resource preemption on the site should be eliminated, until the resource levels are great enough to power oak fiefspace expansion. What the exact resource levels required for powering early oak fiefspace expansion is not known, but can be surmised from the resource levels that will not power proper oak fiefspace expansion.

On sites with good productivity levels, many fiefspaces can be maintained. Any fiefspaces below the main canopy that are not from crop trees should be eliminated. This will allow the avaiable resources present to be controlled by crop tree fiefspaces, or to power establishment of new crop tree fiefspaces. The total site photosynthetic array should be cut back to 40-50% densities, emphasizing the area below the main canopy. Once 70-100 crop-tree fiefspaces are present, established, and are beginning their rapid expansion period, during which mortality is not expected, the regeneration manager will need to only cultivate (TSI) the crop tree fiefspaces periodically. Once the crop tree fiefspaces are large enough to control the site, and are being limited by the dominant canopy, then total overstory removal can begin to allow for further crop tree fiefspace

expansion. At this advanced fiefspace size, any shrub component expansion will have a negligible effect on the next overstory.

Understory treatments will be needed for succeeding rotations. Partial overstory removal is dangerous because of the more intense interference present on good sites. If 40-50% of the photosynthetic array and associated fiefspaces can not be removed without thinning the main canopy, then careful attention must be given to insuring crop tree success and weed species inhibition.

On sites with poor productivity levels, few fiefspaces are allowed by the resources available, therefore, some of the main canopy fiefspaces must be eliminated, as well as any understory fiefspaces that are of non-crop species, to allow for new crop tree fiefspace establishment and growth. The canopy should be thinned to maximize the chances of crop tree fiefspace expansion. The level of thinning depends upon the site limitations to resource utilization, but approximately 40-50% of the total site photosynthetic array density should be removed. The 40-50% thinning of the site canopy will allow a greater level of long duration sunflecks and direct sunlight into the regenerating fiefspaces. Shrub control may or may not be required depending on the shrub species and their inherent resource efficiencies, and the

site limitations to fiefspace expansion. Shrub fiefspace control will be needed until each can be dominated or controlled by a crop tree fiefspace.

Once oak fiefspaces are present and expanding, Table 39 lists the constraints that will be in place for approximately the first fifth of the rotation. The major constraints are, again, interference related. Once established and expanding its own fiefspace, biological site characters that maximize interference in the zone below 4.5 feet (1.37 m) are positively correlated with the survival of oak reproduction. The increase in photosynthetically active material below the photosynthetic array of the oak regeneration helps to minimize other tree species from establishing and expanding fiefspaces. The value of the cited litter layer constraint is probably physical in nature due to it acting as a mechanical barrier to other tree regeneration and, especially on poorer sites, of conserving moisture.

Regenerative scenario

A scenario for regenerating oak can now be formulated to provide a regeneration manager with a working model to test. The scenario proposed is an elaboration and expansion of work by Oliver (1978). The scenario is outlined below in

several points. Remember that this scenario is based upon the analyses performed and the observations made, thus this scenario outlines the biological possibilities. Insertion of this scenario into the economic environment needs to be completed before field managers can be expected to adopt the principles involved.

Oak regeneration grows in patches in the forest where resources are available. Table 17 suggests that white oak and sugar maple are very patchy in distribution in the forest while red oak is less patchy and more widespread. Any time oak reproduction is present, cultural techniques should be used to maximize the probability for its continued survival. Oak regeneration should be released where it is found by elimination of any fiefspace that poses a threat to continual oak fiefspace expansion. Total release from top-canopy domination of oak fiefspaces is not suggested until the oak starts to enter the rapid fiefspace expansion phase at approximately 3 inches (7.6 cm) in diameter. Removal of the overstory will then maximize the probability of oak domination of the site. The staged removal of the overstory suggested here has been defined as a shelterwood. Shelterwood cutting in small patches around the regenerating areas, or the potentially regenerating areas, would be termed, more properly a "group shelterwood" silvicultural

treatment. This silvicultural method allows for the minimization of the interference constraints on oak regeneration.

If advanced oak regeneration is not present, oak reproduction in a stand can be potentially initiated by the group shelterwood. The shelterwood would be initiated in areas where there are potential oak seed producers. The treatment could be maximized in effect if completed less than one and one-half years before a large acorn crop. The group shelterwood should remove approximately 40-50% of the canopy cover, especially in the understory. Thinning from above should leave the 15-23 inch DBH oak classes for seed production. Thinning from below should be completed to remove interfering tree species on the site and to eliminate the importance of the shrub component. Herbiciding would be a potential mechanism for shrub control.

By the third or fourth year, if no oak regeneration is present, direct seeding or planting could be initiated. Direct seeding practices must be able to break-up the litter and bury the acorn in the mineral soil and then provide cover. Planting should be with the largest root size nursery transplant stock available. Theoretically, three times the expected number of crop-trees at the end of rotation need to be planted if no further site treatments

are planned. With single stem care, one and one-half the expected number of trees should be planted. This will allow for chance mortality and phenotypic selection of the growing stems. Direct seeding or planting will still require interference minimization, especially in the light resource zone below 4.5 feet. An experimental approach capitalizing on the life-history and evolutionary development of oak would be to mow off the tops of the oaks to be planted while in the nursery and then plant the root stock. The precise nursery regime would depend on equipment, time of mowing, time of lifting, and probably require spring planting. Herbicides could be sprayed on the planting area at the same time, lending the planting system to single unit mechanization.

Direct seeding of acorns could mimic natural mechanisms. Planting acorns beneath the litter eliminates one of the critical portions of the life-cycle of oak, specifically the catchment and lodging in a safe site for germination. Scarifying the immediate area of planting eliminates barriers to acorn growth while maintaining some control of other interfering species. Catchment sites where litter and acorns gather through actions of water, wind, and gravity usually have successful regeneration present if the site does not run through large amplitude wet and dry

cycles. Direct acorn planting would eliminate the chance lodging probabilities and increase the chances of a seed landing in a safe site. If reliable seed sources could be found, coupled with a functional pest repellent, natural fluctuations in acorn production and acorn consumers could be damped and therefore, seed pest problems minimized.

Any silvicutural treatment in an oak stand to maintain or regenerate oak must follow a few ecological rules. The primary rule is to favor the crop-species and to inhibit the non-crop species wherever their fiefspaces interact. With constant reproduction, constant stand treatment will be needed to continue the pressure against non-crop trees. Periodic cleanings or thinnings will be required throughout the life of the stand to maintain the domination of the available resources by selected fiefspaces and to insure regeneration of the next stand. Harvesting without subsequent treatments has lead to the problems experienced today in eastern Iowan woodlands. Continual pressure against interfering fiefspaces is the only method to viably reproduce oak in eastern Iowa. The reason is buried in the oak species and in the forest history of eastern Iowa.

The forests of Iowa were "scattering timbers", or oak-prairie parklands, when European settlers arrived. Through highgrading and fire prevention, the forests slowly began to

resemble the more diverse and lush forests of the eastern United States. Unfortunately for later regeneration managers, the natural selective processes upon the oaks that eventually genotypically remained in Iowa, were developed around the oak parkland type of forest, especially in the case of white oak. The oak populations present in eastern Iowa could be assumed to be better adapted to the open growth forests of the prairie-forest edge, than the dense, closed understory forests of farther east. The population of oak now in eastern Iowa has been selected throughout the glacial expansions and contractions for prospering in the lower moisture levels of the forest fringe. Eastern Iowa oaks were associated with the parkland growth regime where the trees are surrounded by grasses and pockets or islands of deeper forest plants which were kept within the distinct confines of cove sites and lower topographic position features on the plains and along stream valleys. The ancient forests had a low density of stems per acre and an open understory. Fire prevention and highgrade logging produced these stands.

Sugar maple, a master interferer, was selected for under conditions of strong biological interference in the eastern and southern United States. Before settlement the sugar maple could not successfully colonize and dominate the

canopies of eastern Iowa forests because the physical site constraints within the open parkland forests selected against its regeneration. Large fluctuations in microclimate factors, especially regarding water relations, coupled with top-death from fire, favored the oaks and inhibited sugar maple. With settlement, fire control and massive harvesting (disturbance) lead to large amounts of resources becoming available, and therefore, regeneration flourished. The natural pressures against sugar maple were removed.

The silvicultural system suggested here is focusing on the original pressures that helped form the original oak forests in eastern Iowa. In place of fire, cultural treatments are being inserted. Fire could be a valuable tool in eastern Iowa but extensive tests are needed with a periodic fire regime. In summary, the later into the twentieth century we proceed, the more like the early eighteenth century our regeneration ecology must be to viably regenerate oak.

Any stand that is going to be regenerated will have many limitations to oak reproduction. All limitations must be appreciated in order to be successful. To maximize the probability for success, the regeneration model (Figure 2) can be used as a check list. If the site has the heavy

maple-type litter layer, it must be broken up to provide catchment and germination factors for oak to occur. The fiefspace interference may be too great on the site, therefore, resources need to be released by stem removal. Many factors will affect the regeneration and a regeneration manager must be flexible enough to fit cultural treatments to each site.

Scenario summation

A summary of the biological regime needed for the proper regeneration management of oak forests begins with determining the presence or absence of advanced regeneration. If advanced regeneration is present on the site greater than 70-100 stems per acre (175-250 stems per hectare) and at least 3 inches (7.6 cm) in diameter then the overstory can be removed. Fiefspace maintenance will be required.

If little advanced regeneration is present, any regeneration should be favored by group shelterwooding around the regenerating areas and around potential seed producers. Relatively intensive fiefspace maintenance will be required until the proper amount of regeneration is present on the site. Through the life of the stand, fiefspace maintenance will continue to be required to prevent regeneration failure at the next harvest.

If no advanced regeneration is present, group shelterwood harvests should be used among and around the patches, groups, or individuals that would be good potential seed producers. Piefspace maintenance needs to be performed intensively until regeneration is present, then periodically throughout the life of the stand. If advanced regeneration is still not present, and does not appear after 3-4 years, then artificial reproduction should commense.

The term "piefspace maintenance" is both the identification and minimization of site limitations. The major site limitations will be specific to each site and could be comprised of single or multiple site factors and/or their interactions. For example, the presence of a heavy maple litter layer, interference from piefspaces below 4.5 feet (1.37 m) tall, and interference from an intermediate canopy zone could all occur on one site. The stock treatment of one constraint may still leave the oak reproduction inhibited or prevent oak piefspace establishment and expansion. Each site will require a specific regeneration prescription based on the dominant reproductive constraints present. Piefspace maintenance is the act of treating the individual oak piefspaces to maximize their potential for expansion, or if no oak piefspaces are present, to maximize the potental for site colonization by oak.

"Group shelterwood" is the removal of approximately 40-50% of the canopy on a normally stocked or overstocked stand. On understocked stands, cutting back to 40 square feet of basal area might be a bench mark to attain. Be aware that there will be a trade-off between biological modification (protection) of the site and resource release. Poorer sites may require less cutting than good sites to minimize the limits caused by physical environmental extremes. Group shelterwooding should be established on areas one-half to 2 acres (0.2-0.8 ha) in size where the probabilities of regenerating oak is great. If there is no oak seed source in the area, artificial reproduction should be used. The shelterwood pocket should be an open, parkland-type area. Continual treatment will be required on the site to protect oak fiefspaces for 5-7 years. Periodic oak fiefspace enhancements could then occur every 10 years over the life of the stand. New regeneration of oak through the life of the stand can be utilized to convert to an all-age forest of even-aged patches of oak, or only the regeneration occurring in the last few decades of the rotation could be considered as the next set of crop-trees. Waiting until the end of the rotation to regenerate oak has not worked, but periodic fiefspace management throughout the rotation will maximize the probabilities for regenerative

success. Once stands are converted tc this silvicultural regime, fiefspace management will tecone progressively easier over time. The poor regenerative state of the current stands has been purchased by inattention and abuse over a century and can not be reversed overnight.

CONCLUSIONS

The major conclusions from this dissertation are that oak must be regenerated by maximizing the probability of reproduction of oak while minimizing the reproduction of sugar maple through individual stem treatments, and that regeneration managers need to manipulate resource availability to crop stems.

Specifically, a group shelterwood system whose residual site qualities mimics the site qualities found in eastern Iowa forests before settlement by Europeans will favor oak. But, this system will require continual attention to resource management since recurrent disturbance/stress pressure will be required to prevent more interference tolerant species from colonizing and dominating oak sites. To increase the probability of regenerating oak, the following contraints should be appreciated and managed for:

1) Light - More light resources must be made available to the soil surface to power oak fiefspace establishment and expansion.

2) Space - Physical room for fiefspace establishment and expansion must be allowed for individual stems of oak.

3) Continual treatment - A constant disturbance/stress pressure must be maintained against non-crop species on oak sites.

The components of the regeneration model (Figure 2) all need strengthening, especially at the micro-climate (physiological ecology) level. More information on the factors controlling flowering and fruiting, both internal and external, are required. Also, cultural treatments need much further research. The misting of herbicides and the use of grazing and fire all can play a role in managing oak woodlands, but careful testing is required. Artificial regeneration production, grading, and planting procedures need to be evaluated and implemented. Finally, a large study needs to be completed to produce the actual field guidelines, or the quantifiable stocking, mortality, density, and treatment response measures found in the oak regenerating forests of eastern Iowa, that this study has only suggested might be of importance.

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To summarize graduate education:

"The human mind has first to construct forms independently before we can find them in things. Knowledge arises from the comparison of the inventions of the intellect with observed fact."

Albert Einstein

Thanks Mom and Dad!

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